Vol. 5 SEPTEMBER · 1942 No. 3

LLOYDIA

A Quarterly Journal of Biological Science

Published by the Lloyd Library and Museum, Cincinnati, Ohio

A Contribution Towards a Monograph of the Genus Oidium[1] (Fungi Imperfecti)

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The genus *Rhinotrichum* (= Oidium) has for some years been of considerable interest to the writer because of the fact that it was early discovered that in order to determine members of this group, as in many another of the Fungi Imperfecti, it is necessary to monograph the genus on a worldwide basis. It was also found that the genus probably represents the conidial phase of Basidiomycetes since in certain species clamp connections were found in the septa of the conidiophores, although it was not until later that definite connections were made between the conidial and basidial phases.

The early studies demonstrated that the older species were often misinterpreted or greatly broadened, and in the various herbaria they frequently included a heterogeneous lot of specimens. Therefore, while studying in Europe, the older species were studied, and especially those deposited in the British Museum of Natural History and in the Kew Herbarium where the Berkeley and Cooke types of *Rhinotrichum* are deposited. Since that time, however, because of other duties, the monographic studies were postponed, although specimens were assembled and the literature was perused more carefully. These two factors, it is felt, have made it possible to make more complete the present paper and to place the species on a firmer basis. There are undoubtedly other species in other genera which need still to be transferred to the genus that now, as will be shown, must be transferred to the genus *Oidium* which supersedes *Rhinotrichum*. The genus *Monilia* in its older, broader and more unsatisfactory status, probably contains additional species, as is also true of *Oospora*. Even the genus *Oidium* has not been completely studied because of the impossibility at this time of examining type material. In view of the present world condi-

[1] Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, No. 159.

tions with the accompanying uncertainties, it seems advisable to publish the results of the present studies, made over a period of years, in the hope that a contribution may be made to the taxonomy of the Fungi Imperfecti.

The members of the genus *Oidium* have been variously distributed in a number of genera of the Fungi Imperfecti, among which may be listed *Monilia*, *Olpitrichum*, *Rhinocladium*, *Rhinotrichum*, and *Zygodesmus*. As the synonymy under the different accepted species will demonstrate, this is but a partial list and accordingly is only indicative of the confusion that exists in regard to this and related genera. Reasons for this confusion are to be found in the gradual accumulation of knowledge which has resulted from the study of an increasing number of forms that have been placed with difficulty in the existing inadequately described and often poorly illustrated genera. Not all taxonomic difficulties, however, have resulted from insufficient original descriptions since a considerable proportion has also resulted from the blind following of Fries and Saccardo, who, it would seem, often failed to comprehend the descriptions and limits of the genera proposed by their contemporaries or predecessors, and arbitrarily established their own and not infrequently erroneous concepts. These factors of inadequate description and of faulty compilation, together with the attempt to fit increasing numbers of forms into a system that was not based on sufficiently comprehensive studies, have resulted not only in an excessive number of mixed genera, but also in certain genera coming to contain all those forms that may have had any semblance, fancied or real, to the original scanty definitions.

The first genus to be described which would include those species that are now treated in *Oidium*, is *Acladium* of Link (Mag. Ges. Naturforsch. Freunde z. Berlin **3**: 11–12. 1809) whose description follows:

> "Caespitulis densis, floccis ex olivaceo et luteo-albis; sporidiis ovalibus hinc inde adspersis. Caespitulis initio parvi dein ad unc. et ultra latitudine effusi, oculo nudo tomenti instar tenuissimi apparent. Color exsiccati albescit. Flocci sat magni et sporidia magna in hoc ordine. Sat persistet. Frequens in truncis arborum emortius. Et e Lusitania hab mus. Iconum V, fig. 13."

Melin and Nannfeldt (Svenska Skorgsvardsför. Tidskr. **1934**: 451–452. *fig.* 37. 1934) have examined an authentic specimen of *Acladium conspersum* that was sent to Fries by Link who had determined it. These later students not only were convinced that this was a species of *Rhinotrichum*, but also furnished drawings of the conidiophores and conidia to substantiate their findings. At the same time they furnished measurements of the spores and thus they have made it possible to compare it with a species that is known today, but under the names of *Rhinocladium olivaceum* Bres. or *Rhinotrichum repens* Pr. Although there is now little doubt as to the original interpretation of the genus *Acladium*, the name unfortunately can not be employed since Fries (Syst. Myc. **3**: 415. 1829) reduced *Acladium* to synonymy under *Sporotrichum*. Not only is the name untenable, but it means that for those species which have been allocated

to this genus by medical mycologists, a place must be found elsewhere.

In the same publication with *Acladium* and only five pages later, Link also described the genus *Oidium* as follows:

> "15. *Oidium. Thallus e floccis caespitosis, septatis, ramosis, decumbentibus; apicibus articulatis: articulis in sporidia secedentibus.*
>
> Thallus e floccis complicatis, sporidiis inspersis magnis ovalibus, ita ut Sporotricho aut Geotricho affine credideris genus. Cum vero accurate inspexeris floccos, invenies apices articulatos, articulosque separari et thallo inspergi. Unica species, colore pulchre aureo, O. aureum (Trichoderma aureum P.) cujus iconum V. fig. 29."

Link's description is sufficiently general to include all those forms that have been placed in the genus since its founding. However, were it not for Corda's illustration of the type species [under *Torula aurea* (Lk.) Corda] it would be impossible to typify either the species or the genus. Fortunately the writer has had available for study a recent collection that matches Corda's figures and it is possible to state, providing Corda's synonymy is accurate, and such seems for the most part to be the case, that the majority of those species that have been placed in the genus *Rhinotrichum* by Saccardo (Syll. Fung. 4. 1886 *et seq.*), Sumstine (Mycologia 3: 45–56. 1911) and others must now be combined under *Oidium* which although pre-Friesian was adopted by Fries (Syst. Myc. 3: 427. 1829) in its original sense although additional, and in part unrelated, species were added. This present concept of *Oidium*, while perhaps upsetting to mycologists and plant pathologists alike because they have become accustomed to picturing either the conidial stage of the Erysiphaceae or of *Oidium lactis* when the name appears in print, is not new since Sumstine (Mycologia 5: 45–61. 1913) used the name in its proper sense stating that it "resembles *Rhinotrichum* in general appearance and in structure, but differs from that genus in the production of spores. In *Rhinotrichum* the spores are produced singly on the upper divisions of the sporophores, in *Oidium* the spores are produced in chains." This method of distinguishing the two genera, however, cannot be considered a reliable criterion. Indeed, *Rhinotrichum rubiginosum* (Fr.) Sumst., *R. Curtisii* Berk., and *R. ramosissimum* Berk. & Curt., all recognized by Sumstine as belonging in the genus *Rhinotrichum*, produce spores in short, fragile chains and thus negate Sumstine's distinction between the two genera. Even in those species in which catenation of spores is not plainly evident, a careful examination of many individual spores will reveal that there are scars on both ends of a certain proportion of them and this indicates that they were once connected in chains.

As has already been stated above, the genus *Rhinotrichum* as applied by authors subsequent to Corda, is ruled out on the ground of priority. If this were not sufficient grounds for discarding the name as it has been used, then it is only necessary to quote Corda's description of the then monotypic genus to add further proof. Corda describes the type and only species as follows:

"Rh. simplex tab. IV, fig. 232, åcervulis minutis, atris; floccis simplicibus, erectis, rigidis septatis; infra atris, supra fuscis et verrucosis; sporis magnis ovato-acuminatis, fuscis, subdiaphanis, hylo minuto basilari instructis."

The characterization of the colony (*acervulis*) as black, and the conidiophores (*floccis*) as simple, rigid, black below and fuscous and verrucose above, does not describe even remotely the generic characters of any of the species that have appeared in the literature since. Indeed, Saccardo (Syll. Fung. **4**: 91–96. 1886) divided the thirty-one species then known into four color groups that are constituted as follows: *Albidi vel grisea,* 11 species; *Subrosea,* 3 species; *Aurea, fulva, ochracea, citrina,* 16 species; and *Nigricantia,* 1 species which is the type of the genus and with which none of the others agree. It is therefore quite evident that *Rhinotrichum* in the sense of Corda cannot be considered to include those forms that were subsequently placed in the genus, and it is equally obvious that until it is possible to typify Corda's genus in its original sense, it should be considered a *nomen perdubium* which has at present no taxonomic standing. Accordingly, there is no reason to conserve that genus against *Oidium* unless one resort to the unsatisfactory procedure of applying the very unsatisfactory precept of general usage. In favor of the use of *Oidium* in its original meaning are: 1) the genus may readily be legally typified; 2) by thus typifying the genus, the way will be paved for accepting *Sporendonema* of Desmazière (Ann. Sci. Nat. sér. I. **11**: 246. 1827) for those forms represented by *Oidium* or *Oospora lactis* and *casei*, and *Acrosporium* of Nees (Sys. Pilze **2**: 14. 1817) for those species which are the conidial stages of the Erysiphaceae, as has already been proposed by Sumstine (Mycologia **5**: 45–61. 1913). So treated, the various forms will fall into as natural groups as possible in view of the present state of our knowledge; 3) the number of name changes is not excessive and 4) the International Rules of Botanical Nomenclature, if they are to have any force, if the principle of priority is to be maintained, and if the type concept is to persist, cannot be maintained by making constant appeasement to mental laziness. The practice of conservation should be applied only when an original species or genus can not be readily typified or in those cases in which excessive name changing would result in confusion that would prove harmful to the advance of botany as a whole.

For the privilege of studying specimens in herbaria, the writer is indebted to Dr. E. Ulbrich, Herbarium of the Botanical Museum, Berlin-Dahlem (B); Dr. John Ramsbottom, British Museum of Natural History (BM);[2] Professor H. H. Whetzel and H. M. Fitzpatrick, Cornell University (CU); Professor G. W. Martin, Herbarium of the University of Iowa

[2] Abbreviations cited in parenthesis are those listed in Chronica Botanica **5**: 143–150. 1939 and are used in order to obtain uniformity in the citation of specimens. Special herbaria within the institutions given thus (S-Sydow) indicates that the specimen is in the herbarium of Sydow at Stockholm. Private herbaria are indicated by the full name of the owner in ( ).

(IA); Mr. A. D. Cotton, Kew Herbarium (K); Dr. E. B. Mains and Dr. L. E. Wehmeyer of the Herbarium of the University of Michigan (MICH); Dr. G. T. Moore, Missouri Botanical Garden (MO); Dr. Fred J. Seaver, New York Botanical Garden (NY); Dr. H. D. House, New York State Museum (NYS); Dr. Gunnar Samuelsson, Royal Botanical Museum, Stockholm (S); Dr. H. S. Jackson, Herbarium of the University of Toronto (TRT); Mr. J. A. Stevenson, Dr. W. W. Diehl, and Dr. C. L. Shear, Mycology and Disease Survey, U. S. Department of Agriculture (BPI) and Dr. Perley Spaulding, Division of Forest Pathology, U. S. Department of Agriculture, Northeastern Station at New Haven, Conn. (FP). The writer is also deeply appreciative of the cooperation of Dr. D. P. Rogers who has not only furnished many specimens, but has also taken the pains to confirm the writer's findings in regard to the connections between the perfect and imperfect stages as well as to furnish the names for the different basidiomycetous species.

Oidium Link, Mag. Ges. Naturforsch. Freunde z. Berlin 3: 1809; ex Fries, Syst. Myc. 3: 427. ~~1829.~~ 1832

Alysidium Kunze & Schmidt, Myk. Hefte 1: 11. 1817.
Rhinotrichum of authors, not Corda, Icon. Fung. 1: 17. 1837.
Amphiblistrum Corda, Icon. Fung. 1: 11. 1837.
Physospora Fries, Summa Veg. Scand. p. 495. 1849.
Olpitrichum Atkinson, Bot. Gaz. 19: 244. 1894.
Allescheriella P. Hennings, Hedwigia 36: 244. 1897.
Nematogonium Bainier, Soc. Myc. France Bull. 21: 227–228. 1905.

Type species: *Oidium aureum* Link.

The genus *Oidium* may be characterized as follows: the colonies white or grayish to some shade of yellow, rusty red or rusty brown; the vegetative mycelium creeping, septate, often intricately branched to form loose-hypochnoid to relatively dense colonies; the conidiophores erect or ascending, rarely repent, simple, branched or anastomosing, hyaline to colored and translucent, never black or fuscous, septate or nodose-septate; the conidia usually large in proportion to the diameter of the conidiophores, simple, smooth or internally or externally roughened, spherical to ellipsoidal, produced singly or in chains on sporogenous teeth; the sporogenous teeth usually prominent and stout and not infrequently branched, but occasionally present only as prominent scars, the teeth usually formed acropleurogenously on the conidiophores, on modified and often inflated short lateral branches, or on spore-like vesicles.

The species with a few exceptions, are predominently saprophytic and grow on decaying wood, occasionally on old fructifications of members of the Polyporaceae, or on the ground.

The genus as a whole appears to represent the conidial phase of the more primitive Thelephoraceae or Corticiaceae. Among the species, *O. Morgani*, *O. armeniacum*, and *O. effusum* bear numerous clamp connections while *O. pulveraceum* bears fewer and less conspicuous clamp connections (pl. 3,

fig. A). Of the species that do not form clamp connections, and these make up the major part of the genus, there are none that have been proven by cultural methods to be a part of the life history of a basidiomycetous fungus. However, the writer has been able to trace the connection between the conidiophores of *Oidium Curtisii* (Berk.) Linder and *O. candicans* (Sacc.) Linder with the basidia of *Botryobasidium coronatum* (Schroet.) Donk [=*Pellicularia pruinata* (Bres.) Rogers] and *B. vagum* (B. & C.) Rogers [=*Pellicularia vaga* (B. & C.) Rogers] respectively. These observations have recently been confirmed by Dr. D. P. Rogers (in letter of Dec. 29, 1941). In addition to these two species of *Oidium* which have been definitely connected with their basidial stage, *O. conspersum* (Lk.) Linder appears also to be connected with *Peniophora fusispora* Pat., yet although the mycelium of the conidial stage was traced into the basidial areas, it was impossible to trace it to basidia. It is hoped that by future investigations, the relation between the conidial and basidial phases in the life histories of this and additional species may be discovered. At present, and in the light of the meager knowledge that is at present available, the genus *Oidium*, while morphologically somewhat variable, nevertheless appears to be a biologically homogeneous group.

KEY TO THE SPECIES OF OIDIUM

1. Conidia ellipsoid to ovoid (subovoid to globose in *O. tenerum*)........................2
1. Conidia globose or subglobose (globose and obpiriform in *O. aureo-fulvum*).............26
2. Denticles elongate and acuminate; conidia and conidiophores hyaline....................3
2. Denticles cylindrical and truncate, occasionally represented merely by scars; conidia or conidiophores hyaline or colored..5
3. Conidiophores distinct, arising from repent sterile mycelium; conidia larger than $10\times7\mu$...4
3. Conidiophores as short erect or ascending branches of the sterile mycelium; conidia 6.5–10 $\times4.5$–7μ..1. *O. lanosum*
4. Conidiophores slender, not conspicuously inflated at the apices; denticles long (3.5–14.5μ), tapering; vesicles frequently halberd-shaped; conidia (21.5)–27–30–(36)$\times$(14.5)–18–20–(27)μ ....2. *O. macrosporum*
4. Not as above, conidiophores usually clavate-inflated at the terminal, occasionally also at the subterminal cell; conidia 12.5–18–(21.5)$\times$7.2–11–(12)μ.....................3. *O. tenellum*
5. Denticles formed along the entire length of the conidiophores or at least on the upper two-thirds..6
5. Denticles usually confined to one to three terminal cells or to the upper one-third of the conidiophores...10
6. Conidiophores readily fragmenting; colonies bright yellow..............................9
6. Conidiophores not readily fragmenting; colonies some other color or if yellow, then the conidia are not subglobose or are more than 9μ broad.......................................7
7. Colonies compact, small, somewhat pulvinate, later effuse by confluence, rusty red; conidiophores up to 135μ long; conidia thick-walled, ovoid to truncate-pyriform, 21.5–27$\times$16–18–(21)μ..4. *O. simile*
7. Colonies effuse, hypochnoid, white, cream-colored, buff-colored, or with olivaceous tints; conidiophores 200μ or more long; conidia thin-walled.................................8
8. Conidia 12.5–20$\times$9–14.5μ, basally attached to the sporogenous teeth.......5. *O. conspersum*
8. Conidia (27)–30–36$\times$12.5–16.5μ, obliquely attached to the sporogenous teeth.............. ....6. *O. magnisporum*
9. Conidiophores fusing to form H-shaped anastomoses; terminal cells not monilioid inflated; conidia 9–10–(12)$\times$9–11μ...7. *O. tenerum*

9. Conidiophores not as above, the terminal cells monilioid inflated; conidia 9–11(–14.4)×7.2–9μ ....8. *O. pulveraceum*
10. Conidiophores as short, erect, or ascending branches from the repent mycelium; conidia 6.5–10×4.5–7μ........1. *O. lanosum*
10. Conidiophores erect or ascending, distinct, conidia larger........11
11. Conidiophores erect, short-branched above, hyaline to subhyaline; colonies usually white when fresh and drying cream-color........9. *O. candicans*
11. Branching not confined to terminal cells........12
12. Conidia citriform, mostly apiculate at both ends, in branching chains........13
12. Conidia ovate to ellipsoid, apiculate at the base or if at both ends then the apical end is bluntly rounded........17
13. Colonies white, grayish or some shade of yellow........14
13. Colonies rubiginous or a shade of rusty brown........16
14. Colonies white to grayish; conidia 15–20×10μ; on rust sori........10. *O. griseum*
14. Colonies warm buff or with a distinct yellowish color, not occurring on rust sori........15
15. Conidia (19.5)–23.5–25.5×(10)–11–(14.5)μ; the terminal cell of the conidiophore often concolorous with the colored spores........11. *O. aureum*, 12. *O. album*
15. Conidia 11–20×6–8–11μ; the terminal cell of the conidiophore very rarely colored like the conidia........13. *O. ochraceum*
16. Colonies tufted, the conidiophores very short; conidia (18)–20–25–(28)×(9)–11–(14.5)μ........14. *O. hesperidicum*
16. Colonies effuse, the conidiophores extensive, much branched; conidia (11.5)–12.5–15–(18)×(7.2)–9–11μ........19. *O. ramosissimum*
17. Colonies brick-red to dull, rusty brown........18
17. Colonies hyaline to yellowish or some shade of yellow........22
18. Conidiophores of two types: 1) short, hyaline or dilutely colored, branched; 2) elongate, deeply colored, simple........15. *O. biforme*
18. Conidiophores not of two distinct types........19
19. Conidia of two distinct types: 1) broadly ovoid to spherical; 2) obpiriform to irregularly flask-shaped, broadly truncate at the base........16. *O. aureo-fulvum*
19. Conidia not of two distinct types........20
20. Conidiophores up to 1100μ long and with few, short, sharply ascending lateral branches........17. *O. elongatum*
20. Conidiophores shorter, not nearly simple but much branched or anastomosing and with numerous vesicles........21
21. Conidiophores arcuate-anastomosing above........18. *O. rubiginosum*
21. Conidiophores not arcuate-anastomosing above, much-branched, the branches arising nearly at right angles........19. *O. ramosissimum*, 30a. *O. Curtisii var. ovalisporium*
22. Sporogenous teeth stout, conspicuous; vesicles inflated and bearing one or more sporogenous teeth........23
22. Sporogenous teeth slender or as scars on the conidiophores; vesicles lacking or rare........24
23. Vesicles large, acrogenous; colonies arachnoid, "deep colonial buff."......20. *O. vesiculosum*
23. Vesicles large, pleurogenous, rarely acrogenous; colonies hypochnoid, "primuline yellow."........21. *O. pulchrum*
24. Conidiophores more than 300μ long, 3.5–6.5μ in diameter, ascending branching; conidia 12–16×9–12μ........22. *O. gracile*
24. Conidiophores less than 300μ long and mostly 7–12μ in diameter........25
25. Conidia sessile in short chains, mostly on the ultimate cell, less frequently on the upper end of the penultimate cell........23. *O. chilense*
25. Conidia subsessile very rarely in chains, borne on the apical portions of any of the cells of the upper two-thirds of the conidiophore........24. *O. Bloxami*
26. Mycelium and conidiophores with numerous and conspicuous clamp connections........27
26. Mycelium and conidiophores not as above........29
27. Conidiophores as short branches from the repent mycelium; both conidia and vesicles subtended by clamp connections........25. *O. Morgani*
27. Conidiophores longer than 75μ; spores and vesicles not subtended by clamp connections..28
28. Conidiophores and conidia strongly encrusted........26. *O. armeniacum*
28. Conidiophores not encrusted........27. *O. effusum*

29. Conidiophores simple, or if branched, the branches are short and confined to the upper portion of the conidiophore 34
29. Conidiophores much branched or if few branched, the branches arising at or near the base . 30
30. Conidiophores readily breaking apart at the septa; H-shaped anastomoses numerous . . . . . 7. *O. tenerum*
30. Conidiophores not as above 31
31. Conidiophores spirally twisted 33
31. Conidiophores not spirally twisted 32
32. Colonies "Naples Yellow" or "Antimony Yellow"; conidiophores with dentricles pleurogenous, one or more on each cell; conidia of one type, globose . . . . . 28. *O. sphaerosporum*
32. Colonies rust-colored or "Sanford's Brown," occasionally with yellowish margins; conidia of two types: 1) spherical or broadly ellipsoid; 2) obpiriform to irregularly flask-shaped with broad truncate bases . . . . . 16. *O. aureo-fulvum*
33. Conidiophores hyaline or yellowish below, the terminal cells and the conidia differentiated by their deeper color; colonies "Ochraceous Tawny" . . . . . 29. *O. laevisporum*
33. Conidiophores mostly yellowish brown or fulvous, the conidia concolorous or nearly so; colonies "Tawny," "Sanford's Brown" or rusty brown . . . . . 30. *O. Curtisii*
34. Conidiophores up to 750μ long, simple or short-branched above, anastomoses very rare . . . . . 31. *O. tomentosum*

1. **Oidium lanosum** (Cooke) Linder n. comb.

Clinotrichum lanosum Cooke, Pop. Sci. Rev. **10**: 10. *pl. 68, fig. 1–3.* 1871
Rhinotrichum lanosum Cooke, Handb. Brit. Fungi **2**: 591. 1871
Rhinotrichum parietinum Saccardo, Soc. Myc. France Bull. **12**: 79. *pl. 7, fig. 2.* 1896

Plate 1, Figs. A–B.

Colonies white to dilute ochraceous or "warm buff" (R),[3] effuse, cespitulose to hypochnoid. Sterile mycelium repent, hyaline, branched, anastomosing, septate, 3.5–6μ in diameter. Conidiophores simple, erect, or as ascending branches or the ascending ends of the sterile mycelium, 0– to 2-septate, somewhat inflated, 27–81$\times$4.5–7.2μ with seldom more than one or two branches, the terminal cells apiculate. Vesicles few. Sporogenous teeth acro-pleurogenous, minute, tapering-truncate, 0.5$\times$0.5–2μ. Conidia hyaline to light colored, ovoid, 4.5–7$\times$6.5–10μ, often minutely apiculate at the base, occasionally in short chains.

Specimens examined: ENGLAND, Holloway, March 1870, in Cooke, Fungi Britannici exsiccati, *356*.**Type** (K, BM, FH) and in Vize, J. E., Micro-fungi Britannici, *77, 579.* (MO, FH); Kew, on damp walls in storehouse, Feb. 23, 1911, *E. M. Wakefield* (K): ITALY, Padua, *P. A. Saccardo* (from description, specimen not available).

This is the smallest species of *Oidium* and may readily be distinguished by the small, branch-like conidiophores and the small spores. Excepting for the dimensions, the species resembles *O. tenellum* when this latter species is grown on artificial media where it produced its conidia on short, erect conidiophores that arise as side branches from the repent mycelium.

Saccardo's figure and description of *Rhinotrichum parietinum* agree in all respects with *O. lanosum* and accordingly there is little doubt of its being a synonym of the latter.

[3] Colors included within quotation marks are those of Ridgway, R. Color Standards and Color Nomenclature. Washington, D. C. 1912.

2. **Oidium macrosporum** (Farlow) Linder n. comb.

Rhinotrichum macrosporum Farlow, in Saccardo, P. A., Michelia **2**: 148. 1880
Olpitrichum carpophilum Atkinson, Bot. Gaz. **19**: 244. *pl. 23*. 1894
Olpitrichum macrosporum (Farl.) Sumstine, Mycologia **3**: 55. *pl. 39, figs. 7–11*. 1911.
Plectothrix globosa Shear, Torrey Bot. Club Bull. **29**: 457. 1902.

Plate 1, Figs. G–H.

Colonies effuse, hypochnoid or cottony, white to "cream buff" (R). Conidiophores 360–720×7.2–9μ at the base, 3.5–5.5 at the apex, hyaline, erect, slender, few-septate, simple or sparsely long-branched below, the branches arising at right angles, or short-branched above, the branches a result of the proliferation of the sporogenous teeth in the apical spore bearing area. Denticles long, tapering to a slender truncate apex, 3.6–14.5×2–3.5μ occasionally continuing to form long or short branches which in turn bear sporogenous teeth and, not infrequently, halberd-shaped or irregularly shaped vesicles. Conidia hyaline, smooth, ellipsoid subglobose, (21.5)–27–30–(35)×(13)–18–20–(22)μ.

Specimens examined: UNITED STATES, VIRGINIA, Radnor Heights, on dead bark of privet (Buxus), *C. L. Shear* (BPI, slide FH); ALABAMA, Lee County, Auburn, on cotton bolls, Oct. and Nov. 1890, *G. F. Atkinson, 1775, 1779* (FH, CU); LOUISIANA, on cotton bolls, *C. V. Riley*, **Type** (FH, NY, BM); KANSAS, Topeka, on *Liriodendron tulipifera*, Oct. 20, 1926, *E. Bartholomew* (FH); CUBA, on cotton flowers in laboratory culture, Dec. 1903, *R. Thaxter* (FH).

This species has also been reported from New Jersey by Dr. C. L. Shear to whom the writer is deeply indebted for his suggestion that *Plectothrix globosa* might be a synonym of *Rhinotrichum macrosporum* Farlow, [=*Oidium macrosporum* (Farl.) Linder]. A comparison of the slide sent by Dr. Shear shows that this specimen produces spores that are more constantly globose or subglobose than are those of *O. macrosporum*, but since this slide was made from material that had been grown on an artificial substratum, it would seem that spore shape may be a result of its influence, especially since in nature, spore size and shape are somewhat variable.

This species is one of the few that appears to be weakly parasitic. Shear (Tech. Bull. U. S. Dept. Agric. **158**: p. 22, 1931) lists it among the forms that may do damage to *Vaccinium macrocarpon*, and Walker (Univ. Florida Agric. Expt. Sta. Bull. **214**: 26. *fig. 11*, 1930) reports that this species, in association with *Rhinotrichum tenellum*, occurs as a saprophyte or weak parasite on cotton in Florida.

3. **Oidium tenellum** (Berk. & Curt.) Linder n. comb.

Rhinotrichum tenellum Berk. & Curt., Grevillea **3**: 109. 1875.
Rhinotrichum cucumerinum Berk. & Curt., Grevillea **3**: 109. 1875.
Gonatobotrys tenellum (Berk. & Curt.) Sumstine, Mycologia **3**: 54. 1911.
Gonatobotrys cucumerinum (Berk. & Curt.) Sumstine, Mycologia **3**: 45. 1911.

Plate 1, Figs. E–F.

Colonies white to cream-colored, cottony to pilose. Conidiophores up to 300μ long, 7–12μ in diameter at the base. hyaline, erect or ascending, at

EXPLANATION OF PLATES

All drawings have been made with the aid of the camera lucida, and unless otherwise specified, the conidiophores are illustrated at a magnification of ×285 and the conidia at a magnification of ×400. Units of the scales equal 10μ.

PLATE I

FIGS. A–B. *Oidium lanosum* (Cke.) Linder, showing the short, branch-like conidiophores arising from the repent mycelium. Drawn from the type specimen.

first simple or occasionally sparsely short-branched, the terminal or subterminal cells slightly to conspicuously inflated, club-shaped to clavate, 9–18μ in diameter. Sporogenous teeth confined to the terminal or the inflated cells, 3.6–13μ × 1.5–2μ, tapering, straight or curved. Conidia hyaline, smooth, ellipsoid, 12.5–18–(22) × 7.2–10.5–(12)μ, frequently apiculate at the base.

Specimens examined: UNITED STATES, SOUTH CAROLINA, on rotton onion, *Ravenel*, **Type** (BM, FH); on Indian corn, *Ravenel*, type of *R. cucumerinum* Berk. & Curt. (BM, FH); ALABAMA, Lee County, Auburn, on cotton bolls with *O. macrosporum* (Farl.) Linder, Nov. 1890, *G. F. Atkinson, 1779* (FH, CU); BRITISH EAST AFRICA, Tanganyika, culture from *Sorghum* sp. communicated by E. W. Mason (FH, Imp. Myc. Inst.).

In addition to the above stations, Walker (Univ. Florida Agric. Expt. Bull. **214**: 26. *fig. 11.* 1930) reports the species from Florida where in association with the preceding species it grows as a saprophyte or a weak parasite on cotton.

The elongate tapering sporogenous teeth and the clavate inflated terminal cells mark this species off at once as distinct from other members of the genus. The inflation of the terminal and less frequently of the subterminal cells, however, gives this fungus the appearance of a member of the genus *Gonatobotrys*. If this species is compared with *O. lanosum*, it will be observed that excepting for the dimensions of the structures, there is a close resemblance between the two species. Furthermore, *O. tenellum* when grown on artificial media as potato dextrose agar, loses its characteristic appearance and tends to become slender, thus resembling *O. macrosporum* (Farl.). It is for this reason that it seems best, in the light of present knowledge, to consider this species an extreme modification of the morphology that is typical of members of the genus *Oidium*, rather than to transfer it to *Gonatobotrys* to which it only has a superficial resemblance.

4. OIDIUM SIMILE Berk., Journ. Bot. 4: 310. 1845.

Gymnosporium fulvum Berk. & Curt., Linn. Soc. Journ. **10**: 355. 1868.
Rhinotrichum fulvum Berk. & Curt., Grevillea **3**: 108. 1874.
Chromosporium fulvum (Berk. & Curt.) Saccardo, Syll. Fung. **4**: 6. 1886.
Coniosporium fulvum (Berk. & Curt.) Pound & Clements, Minn. Bot. Studies **9**: 660. 1896.
Allescheriella uredinoides P. Henn., Hedwigia **36**: 244. 1897.
Hyphoderma zeylanica Petch, Roy. Bot. Gard. Peradeniya Ann. **6**: 349. 1917.

FIGS. C–D. *Oidium conspersum* (Lk.) Linder. The ellipsoid and slightly apiculate conidia (C), and the conidiophores (D) illustrating the characteristic branching and the distribution of the sporogenous teeth. Pointing downward is a simple conidiophore that has arisen from the repent vegetative mycelium.

FIGS. E–F. *Oidium tenellum* (B. & C.) Linder. Typical conidiophores with the elongated sporogenous teeth arranged around the apical portions of the clavate-inflated terminal or subterminal cells. Drawn from type material.

FIGS. G–H. *Oidium macrosporum* (Farl.) Linder, showing the simple conidiophores with long, curved, and tapering sporogenous teeth and, above, a conidiophore on which the sporogenous teeth have proliferated. Drawn from type material.

Plate 4, Fig. B.

Colonies compact, small, somewhat pulvinate at first but later by confluence becoming effuse, at first ochraceous, later becoming fulvous. Sterile mycelium colored next the substratum, anastomosing and closely interwoven, the upper portions lighter colored, yellowish under the microscope. The conidiophores hyaline or very dilutely colored, septate, sparsely ascending branched, up to 135μ long, 3.5–5.5μ in diameter. Vesicles none. Sporogenous teeth short, truncate or else evident as scars. Conidia broadly ellipsoid or subsphaerical to piriform with a broad truncate base to which is often attached remnants of the sporogenous teeth, smooth to sparsely and inconspicuously warted, at first yellowish but soon becoming rust-colored and finally brick red or chestnut brown, 21.5–27×16–18–$(21)\mu$.

Specimens examined: UNITED STATES: SOUTH CAROLINA, Santee Canal, *Ravenel, 106* (FH-C, BM); Society Hill, Sept. 1849, *Curtis, 2296* (FH-C); OHIO, *Lea 147*, **Type** (BM); Terrace Park, Nov. 1929, *M. Fulford* (FH); ALABAMA, Montgomery, *R. P. Burke, 138* (MO 10972); LOUISIANA, Lafayette, Oct.–Dec. 1932, *Bro. Neon, 1807* (FH); BERMUDA, Paget Marsh, Mar. 26, 1922, *H. H. Whetzel* (FH, CU); CUBA, Jan. 1857, *Ch. Wright* (FH-C); JAMAICA, Port Antonio, Apr. 26, 1906, *A. E. Wight, 300* (FH); PUERTO RICO, Rio Piedras, Jan. 19, 1916, *H. H. Whetzel, 20* (FH, CU); TRINIDAD, La Sieva Valley, Port-of-Spain, *R. Thaxter* (FH); VENEZUELA, Caguita, Jan. 5, 1928, *H. Sydow* in Fungi Exotici Exsiccati *880* (FH); BRAZIL, two collections by *E. Ule* (FH); URUGUAY, Santa Lucia, *G. Herter, 78917*, in Plantae Uruguayensis no. *205* (FH).

Oidium simile is quite distinct from all other species in the genus and may readily be determined by its *Uromyces*-like conidia with their thick reddish-brown walls, and by the characteristic compact pulvinate colonies of a brick-red or chesnut-brown color. It is very often difficult to discern the conidiophores of this species since they apparently deliquesce or break up with age. It is only in the younger portions of the mature colonies or in the very young colonies that the conidiophores and the attachment of the conidia may be studied. In spite of the marked characters of this species, it has been confused with *Monilia aureo-fulva* which may be distinguished under the hand lens by the looser cottony appearance of the effuse colonies, while under the microscope the morphology of the persistent conidiophores and of the conidia (pl. 4, fig. G) furnish added means of determining the species. The confusion in regard to the status of the two species has resulted from the fact that Ellis in the North American Fungi, 381, and Rabenhorst in the Fungi Europaei, 2685, issued the same material as *Oidium simile* Berk. and on the labels cited *Monilia aureo-fulva* Cke. & Ellis as synonymous. A study of the type specimens of the two species makes it clear that they are distinct and that the specimens issued by Ellis and Rabenhorst are *M. aureo-fulvum* and not *O. simile*. *Physospora rubiginosa* has also been confused with this species, primarily, it would seem, because of the color of the colonies, but also perhaps because the species has not been clearly defined.

5. **Oidium conspersum** (Link) Linder n. comb.

Acladium conspersum Link, Mag. Ges. Naturforsch. Freunde z. Berlin **3**: 11–12. *pl. 1, fig. 13*. 1809.
Sporotrichum conspersum (Link) Fries, Syst. Myc. **3**: 419. 1829.

?*Amphiblistrum hypochnoides* Corda, Icon. Fung. **1**: 11. *pl. 3, fig. 167.* 1837.
Rhinotrichum repens Preuss, in Sturm, Deutschl. Fl. Abt. III. **6**(25–26): 43–44. *pl. 22.* 1862.
Rhinotrichum sulfureum Ellis & Everhart, Torrey Bot. Club. Bull. **11**: 18. 1884.
Rhinocladium olivaceum Bresadola, Fungi Tridentini **2**: 106. *pl. 217, fig. 3.* 1900.
Rhinotrichum bicolor Sumstine, Mycologia **3**: 50. *pl. 38, fig. 13–15.* 1911.
Rhinotrichum Noblesiae Sumstine, Mycologia **29**: 250. 1937.

Plate 1, Figs. C–D.

Colonies effuse, tomentose to hypochnoid, white, cinereous, cream-color to alutaceous or light olivaceous, the margin often lighter in color. Sterile mycelium creeping, hyaline, branched, sparsely anastomosing, 6–9μ in diameter. Conidiophores erect or suberect, occasionally somewhat flexuous, hyaline or subhyaline, up to 360μ long, 6–10.5μ in diameter near the base, slightly tapering upwards to 3.6–7.2μ, the apex bluntly to subacutely rounded, either smooth or with a terminal denticle, simple above, long-branched or anastomosing below, the branches arising at nearly right-angles and quickly ascending. Sporogenous teeth conspicuous, stout, truncate, 1.8$\times$1.5–5.5μ, usually produced on all cells above the basal branches. Vesicles rarely present. Conidia hyaline to yellowish under the microscope but usually concolorous with the conidiophore while still attached, obovate to ellipsoid, rarely subglobose, apiculate at the base, the wall smooth or minutely internally pitted, (12.5)–14.4–18.2–(20)$\times$(8)–10.8–15–(19)μ.

Specimens examined: EUROPE, GERMANY, Prov. Brandenburg, Triglitz, on decaying wood and bark of *Betula* sp., Oct. 26, 1906, *O. Jaap* (B); Triglitz, on *Betula alba* L., Aug. 15, 1907, *O. Jaap*, in Fungi Sel. Exsic. *296* as *Rhinocladium olivaceum* Bres. (FH); ex herb. Fuckel, *2512*, in Herbier Barbey-Boissier, *114* (FH); PORTUGAL: S. Fiel, *C. Torrend* in Fungi Sel. Exsic., *194*, as *Rhinotrichum sulfureum* (FH); CANADA: NOVA SCOTIA, Colch Co., Upper Brookside, July 20, 1929, *L. E. Wehmeyer*, *206* (FH, MICH); ONTARIO PROV., Hatchley, on *Acer* spp., Aug. 27, 1934 and Oct. 25, 1935, *R. F. Cain* (FH, TRT-8038, 8039, 8040); Lake Temagami, on *Populus* sp., Aug. 8, 1931, *H. S. Jackson et al.* (FH, TRT-3200); Lake Temagami, on *Fraxinus* sp., Sept. 2, 1935, *R. Biggs* (FH, TRT-8044); Lake Temagami, on *Abies balsamea*, Sept. 14, 1933, *R. F. Cain* (FH, TRT-8042); Maple, on *Populus* sp., Nov. 2, 1935, *H. S. Jackson* (FH, TRT-8041); Aurora, on *Populus* sp., Oct. 21, 1931, *H. S. Jackson* (FH, TRT-8043); UNITED STATES, MAINE, Kittery Point, May 1885, June 1886, July 12, 1922, Sept. 1922, all *R. Thaxter* (FH); NEW HAMPSHIRE, Chocorua, July 1917, Sept. 1918, *W. G. Farlow* (FH); MASSACHUSETTS, Canton, in hollow apple stump, May 6, 1923, Oct. 1933, *D. H. Linder* (FH); Canton, on decaying birch log, Dec. 5, 1922, *D. H. Linder*, *265* (FH); Chestnut Hill, April, *R. Thaxter* (FH); East Billerica, Nov. 6, 1900, *Bogne* (FH); East Lexington, Oct. 3, 1901, *C. Bullard* (FH); Hamilton, Oct 5, 1940, *D. P. Rogers* (FH); Hyde Park, Oct. 1901, *C. Bullard* (FH); Milton, on inside of beech trunk, Nov. 1934, *D. H. Linder* (FH); Sharon, on apple wood, Mar. 1916, *A. P. D. Piguet* (FH); Sharon, on decaying oak, Oct. 1934 and Nov. 1934, *A. P. D. Piguet* (FH); Weymouth, Nov. 1885, *J. E. Humphrey* (FH); RHODE ISLAND, Sakonnet Pt., Oct. 11, 1941, *A. M. & D. P. Rogers*, *940*, *941* (FH, Rogers); CONNECTICUT, East Granby, Oct. 5, 1939, *H. G. Eno* (FH, FP8-4247); New Haven, June 1890, *R. Thaxter* (FH-617); Woodmont, Sept. 3, 1884, *R. Thaxter* (FH-2782); NEW YORK, Labrador Lake, May 5, 1936, *W. L. White*, *2466* (FH); McLean, Sept. 5, 1938, *W. L. White*, *3379* (FH, CU-27862); Seventh Lake, Adirondack Mts., Aug. 24, 1934, *G. D. Darker*, *5141* (FH); Syracuse, Oct. 1887, *O. F. Cook* (NY-Ellis); PENNSYLVANIA, Fern Hollow, Alleghany Co., Aug. 5, 1910, *D. R. Sumstine*, type of *Rhinotrichum bicolor* Sumst. (NY, FH); Miller's Gap, Center Co., June 17, 1932, *W. L. White*, *1189* (FH); VIRGINIA, Occoquan, Oct. 10, 1933, *W. W. Diehl* (BPI, FH); NORTH CAROLINA, Grandfather Mt., Sept. 5, 1932, *C. L. Shear* (BPI, FH); FLORIDA, Grassmere, Mar. 1893, *W. G. Sturgis* (NY); TENNESSEE, Burbank, *R .Thaxter* (FH); OHIO, Preston, May 7, 1893 and June 8, 1900, *A. P. Morgan* (IA); MICHIGAN, Ann Arbor, May 1930, *L. E. Wehmeyer*, 40 (FH, MICH);

PLATE 2

FIG. A. *Oidium chilense* Linder. The conidiophores are branched below, and bear on the terminal or subterminal cells, the sessile ellipsoid conidia. From type material.

FIG. B. *Oidium Bloxami* (B. & Br.) Linder, showing the conidiophores and the anastomoses between adjacent members. Vesicles are infrequent and only a single one is shown on the nearly horizontal conidiophore. From type material.

FIG. C. *Oidium rubiginosum* (Fr.) Linder. This species is distinguished by the arcuate, anastomosing conidiophores and the numerous spore-bearing vesicles. From Saccardo, Mycotheca Veneta, *1578*.

WISCONSIN, Madison, Oct. 25, 1882, *W. Trelease, A* (MO); IOWA, Decorah, Oct. 9, 1882, *E. W. Holway, 296*, the type of *Rhinotrichum sulfureum* Ell. & Ev. (NY-Ellis).

Oidium conspersum is morphologically a fairly stable species, but varies in the relative number of sporogenous teeth that are formed on the conidiophores. It is, however, rather variable as to color, the colonies varying from white to olivaceous or alutaceous depending on such environmental characters as exposure to light, the degree of humidity, and the nature of the substratum, as well as on the age of the colonies. It is this variation in color that appears to be the cause of the synonymy in this species. *R. sulphureum* varies from white to light sulfur color; *R. bicolor* from light brown to alutaceous; and *R. olivaceum* from cream color to olivaceous. In those colonies with the darker colors, the spores are usually darker than the conidiophores yet in spite of this apparent difference, the morphology of all the species is the same, and if a sufficient number of collections has been studied in the field as well as in the herbarium, color intergrades are apparent in this widespread and relatively common species. The older synonymy of the species has been discussed in the introductory paragraphs in the course of the consideration of the status of the genus.

The specimens collected at Hamilton, Mass. in October were found growing in company and apparently connected with *Peniophora fusispora* (Schroet.) Hoehnel & Litsch. Since, however, actual connections between the basidia and the conidiophores could not unimpeachably be established, it seems best for the time merely to suggest very strongly that the two forms are genetically related.

6. **Oidium magnisporum** Linder sp. nov.

Plate 2, Fig. D.

Coloniae albae vel dilute cremoricoloratae, effusae, laxe pilosae; hyphis sterilibus repentibus, hyalinis, septatis, ramosis nonumquam anastomosis, 8–9μ in diametro; conidiophoris hyalinis, simplicibus vel ad basem ramosis, usque 500μ longitudine, 8–9μ diametro, cellulis apicalibus 4.5–7.5μ diametro, distanter septatis; denticulis sporogenis simplicibus vel raro ramosis, 1.5×1.5-5.5μ, acropleurogenis, cellulae basales non denticulatae; conidiis ovoideis vel elongatoellipsoideis, sub micros. luteolis et per colore e conidiophoris hyalinis perdistinctis sunt, (27)–30–36$\times$12.5–16.5μ, apiculum quem usque 12.5μ longitudine obliquiterque adjunctum est, excludens.

Colonies white to light cream color, effuse, loosely pilose. Vegetative

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FIG. D. *Oidium magnisporum* Linder. The hyaline conidiophores of this species produce relatively few stout sporogenous teeth which bear obliquely the large light colored spores. From type material.

FIGS. E–F. *Oidium album* Sumstine is characterized by the short and relatively stout conidiophores and the broadly ellipsoid conidia. For comparison with *O. aureum* and *O. ochraceum* see plates 4A and 6A. From type material.

mycelium repent, hyaline, septate, branched and occasionally anastomosing, 8–9μ in diameter, the cells with large vacuoles. Conidiophores hyaline, simple or if branched, only at or near the base, up to 500μ long, 8–9μ in diameter and tapering at the apical cell to 4.5–7.5μ in diameter, the septa few and distant. Sporogenous teeth simple or less frequently branched. 1.5 ×1.5–5.5μ, produced acro-pleurogenously and few to many usually occurring on all but the basal cells of the conidiophores. Conidia ovoid or elongate-ellipsoid, yellow under the microscope and sharply differentiated from the hyaline conidiophore, smooth, (27)–30–36×12.5–16.5μ excluding the obliquely attached apiculus which may be up to 12.5μ long.

Specimen examined: CALIFORNIA, Siskiyou Co., Mt. Shasta, on Shasta fir near melting snow, June 30, 1938, *W. B. Cooke, 10136*, **Type** (FH).

The large spores of this species, with their elongate somewhat obliquely attached apiculus, separate it from *O. conspersum* which it superficially resembles. Also the conspicuous sporogenous teeth are formed less abundantly on the conidiophores but this in itself can not be considered a stable character since some collections of *O. conspersum* may show but few sporogenous teeth while others produce many.

7. **Oidium tenerum** (Sumstine) Linder n. comb.

Rhinotrichum tenerum Sumstine, Mycologia **3**: 51. *pl. 39, fig. 1.* 1911.

Plate 3, Fig. B.

Colonies effuse, thin, hypochnoid or occasionally forming a rather thick layer, light yellow to very dilute yellow at the margins. Conidiophores up to 360μ long, 4.5–9μ in diameter, often slightly tapering upwards, hyaline to dilutely colored, rather frequently though irregularly septate, slightly constricted at the septa at which point the conidiophores may break apart, irregularly and loosely branched, the branches ascending, anastomoses frequent and forming broad H-shaped structures when the conidiophores break up. Vesicles absent. Sporogenous teeth 0.5–5.4×1.5–5.5μ, usually produced on the upper two-thirds of the conidiophores or even almost to the base, irregularly produced in a scattered fashion over the entire length of the cells although occasionally confined to the apical portion. Conidia (9)–10.5–12.5–(14.5)×(9)–10.5–12.5μ, globose to subglobose, apiculate, frequently obliquely attached to the sporogenous teeth, even or the endospore internally roughened, hyaline to dilute yellowish.

Specimens examined: UNITED STATES, LOUISIANA, Jan. 20, 1896, Langlois, **Type** (NY, FH); CUBA, Soledad near Cienfuegos, June 18, 1941, *W. L. White, 274* (FH); Soledad near Cienfuegos, July 9, 1941, *W. L. White, 855* (FH); PANAMA CANAL ZONE, Barro Colorado, Pearson Trail, *T. Barbour, 3* (FH); TRINIDAD, B. W. I., La Seiva Valley, Port-of-Spain, on polypore, *R. Thaxter* (FH); Port-of-Spain, on decayed wood, *R. Thaxter* (FH).

The general morphology of the conidiophores and the disposition of the sporogenous teeth strongly call to mind *O. conspersum* from which *O. tenerum* differs by its globose to subglobose, instead of ellipsoid, conidia. This species also resembles *O. effusum* which however is distinguished by its clamp connections which are evident at each septum. The outstanding character that separates this from all other species in the genus is the H-shaped anastomoses that become quite evident when microscopical preparations are made and the conidiophores break apart at the septa to form H-shaped structures, the abundance of which appears to be dependent to a great extent on the age of the colony.

8. **Oidium pulveraceum** (Ellis) Linder n. comb.

Monilia pulveraceum Ellis, in Craigin, Bull. Washburn College **1**: 69. 1884.
Rhinotrichum pulveraceum (Ellis) Ellis & Everhart, Journ. Myc. **1**: 47. 1885.
Malbranchea pulveraceum (Ellis) Sumstine, Mycologia **5**: 57. 1913.

Plate 3, Fig. A.

Colonies bright yellow, pulverulent to pulverulent-corticioid, effuse. Conidiophores up to 360μ long, 4.5–7.2μ in diameter, hyaline to light yellowish, multiseptate, branching, isodiametric below, the upper cells isodiametric or conspicuously constricted at the septa, somewhat inflated between the septa at which point they tend readily to break apart into one- to several-celled fragments. Sporogenous teeth produced at any point on any of the upper cells and are not restricted to the terminal or subterminal cells, inconspicuous, 0.5–1 $\times$ 0.5–2μ. Vesicles present either as short branches or as enlarged spores with two or more denticles. Conidia 9–11–(14.5) $\times$ 7–9μ, hyaline or light yellow under the microscope, obovoid to ellipsoid, in simple or branched chains, apiculate at one or both ends and frequently laterally denticulate, the primary or basal cell often enlarged and 12.5–14.5 $\times$ 7–9μ.

Specimens examined: NEW JERSEY, Newfield, Nov. 1880, *Ellis, 1658* (NY-Ellis); MISSOURI, Gray Summit, Apr. 10, 1929, *D. H. Linder* (FH); KANSAS, Rockport, *E. Bartholomew* in Ellis & Everhart, N. Amer. Fungi, 2nd ed., *2962*, probably the type distribution (BM, FH, MO).

Of this species, Saccardo (Syll. Fung. **4**: 96. 1886) states: "Vix *Rhinotrichum* ob defectum denticulorum conidiophorum." This is obviously an error since the denticles although small, are plainly evident. The fact that the spores are in chains, that the terminal cells are somewhat inflated and are strongly constricted at the septa, and that the cells readily break apart, does not seem to the writer to be sufficient grounds to return this species to *Monilia* nor to transfer it to *Malbranchea*. The conidiophores of *O. tenerum* also break apart, and the spore chains of all those species of *Oidium* which produce conidia in chains, fragment very readily. It should be recalled that although *Monilia* in the later sense has become very inclusive and has also been split into a number of genera, the original

PLATE 3

FIG. A. *Oidium pulveraceum* (Ellis) Linder. The conidia of this species are borne in chains on definite, though small, teeth on the lower cells and on vesicle-like, inflated, terminal or subterminal cells. Evidence of the formation of clamp connections may be noted at the lower septum.

FIG. B. *Oidium tenerum* (Sumstine) Linder. The numerous H-shaped anastomoses and the readily fragmenting conidiophores are among the characters that distinguish this species. Drawn from type material.

FIG. C. *Oidium candicans* (Sacc.) Linder. The short and usually opposite branches at the apical end of the penultimate and antepenultimate cells of the conidiophores help to distinguish this from related species.

species is the conidial stage of the ascomycetous genus *Monilinia* and should thus be limited if the taxonomy of the Fungi Imperfecti is to have any meaning and if we are to enjoy any semblance of natural classification. In *O. pulveraceum*, clamp connections, although inconspicuous are present to show that this species is the conidial phase of a Basidiomycete and probably associated with one of the species of *Corticium* or of a related genus.

9. **Oidium candicans** (Saccardo) Linder n. comb.

Nodulisporium album Preuss, in Sturm, Deutschl. Fl. Abt. III. **6** (35–36): 101–102. *pl. 93, fig. 51.* 1862, nec *Oidium album* Sumstine, Mycologia **6**: 34. *pl. 116, fig. 11.* 1914.
Monilia candicans Saccardo, Nuov. Giorn. Bot. Ital. **8**: 195. 1876; Fungi Ital. **1**: *pl. 57.* 1877.
Rhinotrichum niveum Cooke & Massee, Grevillea **16**: 10. 1887.
Physospora albida v. Hoehnel, Ann. Myc. **1**: 527. 1903.
Nematogonium album Bainier, Soc. Myc. France Bull. **21**: 227–228. *pl. 13.* 1905.

Plate 3, Fig. C.

Colonies at first white, with age or on drying becoming "Cream Buff" to "Cinnamon Buff," effuse or somewhat tufted, cottony or hypochnoid. Conidiophores 144–500μ long, 7.2–9μ in diameter at the base, 5.5–7.5μ in diameter at the apex, hyaline erect or ascending, simple or sparsely long-branched and anastomosing below, the branches arising at a wide angle and ascending, the ends of the conidiophores often terminating in elongate-ellipsoidal vesicles, 25–36 $\times$ 9–11μ tapering towards the narrow base; the penultimate and antepenultimate cells bear sporogenous teeth and also bear one or two short, vesicle-like branches which arise at right angles to give a cross-like appearance to the conidiophores. Conidia (11.5)–14.5–16.5–(18) $\times$ 8–9–(12)μ, hyaline, catenulate, ellipsoid, apiculate at one or both ends and occasionally bearing lateral sporogenous teeth.

Specimens examined: ENGLAND, Chiswick, June 1887, *G. Massee*, in herb. Cooke, type of *R. niveum* (K) and in Vize, Micro Fungi Britannici, 142 (FH); Richmond Park, Apr. 1933, *E. W. Mason, 1940* (FH); GERMANY, Berlin, Grunewald, Nov. 1906, *G. Lindau* (B); AUSTRIA, Wienerwald, June 1902, *v. Hoehnel*, type of *Physospora albida* (FH-Hoehnel); Nassau, *Fuckel* in Fungi Rhenani, *124*, and in Herb. Barbey-Boissier, *2512* (FH, MO-64287); HOLLAND, Ruurlo, on decayed oak, Sept. 9, 1935, *D. H. Linder* (FH); ITALY, Selva, Sept. 1874, *P. A. Saccardo* in Mycotheca Veneta, *364*, probably type distribution of *O. candicans* (FH); CANADA, ONTARIO PROV., Summerville, May 5, 1933, *H. S. Jackson* (FH, TRT-8078); UNITED STATES, MAINE, Kittery Point, *R. Thaxter* (FH-616, 618, 6697); MASSACHUSETTS, Belmont, on elm wood, Nov. 1925, *D. H. Linder* (FH); Cambridge, on elm wood, Oct. 19, 1892, *R. Thaxter* (FH-620); Milton, Nov. 1925, *D. H. Linder* (FH); NEW YORK, Clarksville, on oak, August, *C. H. Peck* (NYS, MO-15947); McLean Bog, Sept. 8, 1935, *A. M.* & *D. P. Rogers, 954*, connected with *Pellicularia pruinata* (Bres.) Rogers (FH, Rogers); MICHIGAN, Ann Arbor, May 16, 1932, *L. E. Wehmeyer, 47* (FH);

FIGS. D–E. *Oidium hesperidicum* (Sacc.) Linder. The rusty color of the colonies and the tendency of the conidiophores to become fasciculate and anastomose laterally are characters which help to distinguish this species from *O. aureum* (Pl. 4A). From Saccardo, Mycotheca Veneta, *1091*.

FIG. F. *Oidium biforme* Linder. The conidiophores of this species are of two distinct types:—short, hyaline, and branched ones which produce the conidia mostly acrogenously, and elongate and deeply colored ones that may be simple or short-branched and bear conidia acro-pleurogenously. From type material.

OHIO, Preston, wood of *Quercus*, *A. P. Morgan* (FH); IOWA, West Okoboji, on *Populus deltoides*, July 8, 1933, *D. P. Rogers*, *953*, connected with *Pellicularia pruinata* (Bres.) Rogers (FH, Rogers).

This species with its erect, simple or subsimple, conidiophores which bear at right angles either vesicles or short branches on the terminal cell or the subterminal cells, frequently symmetrically and thus giving the general appearance of a crucifix, is readily distinguished from all other hyaline species in the genus. The color of this species is, however, rather variable, ranging as it does from pure white to bright yellow or orange-yellow. Apparently the intensity of the color is to a great degree determined by the abundance of available carbohydrates in the substratum. When the fungus is grown on potato maltose agar with four per cent of maltose, the colonies are "burnt orange" and yet by lowering the concentration of both the potato decoction and the sugar, the amount of pigment produced by the fungus is reduced and the colony is then cream colored. It would thus appear that this factor in part explains variations noted in the field, but it is also possible that the amount of light has some influence. Unfortunately, the culture[4] with which the writer carried on the preliminary studies, died out before the writer was able to complete the investigations of this interesting species.

The species is not only of interest because of the color variations, but also because the writer has been able to trace the conidiophores and their connection with the basidia of *Pellicularia pruinata* (Bres.) Rogers [Syn.: *Botryobasidium coronatum* (Schroet.) Donk]. Substantiation of this finding has recently been furnished by Dr. D. P. Rogers (letter of Dec. 29, 1941) who has traced the connection between the conidiophores and basidia in the specimen studied by the writer (Iowa, W. Okoboji, *D. P. Rogers*, *953*) and also has found the same relation to exist in an additional specimen that he collected in New York (McLean Bog, *D. P. Rogers*, *954*). Thus the species may safely be considered to be the conidial stage of a well-known Basidiomycete.

10. **Oidium griseum** (Sacc.) Linder n. comb.

Rhinotrichum griseum Saccardo, Michelia **1**: 87. 1877; Fungi Ital. **1**: *fig. 63*. 1877.

Colonies floccose, bluish gray to grayish, growing on uredo-sori; hyphae fasciculate, continuous, simple, cinereous, somewhat attenuate above and there denticulate; conidia arising from sporogenous teeth, lemon-shaped or somewhat inequilateral, concolorous with the hyphae, $15–20 \times 10\mu$.

In the sori of *Uredo* on *Rubus*, on the lower surface of the leaves of *Rubus caesius* and *R. fructicosus* in the woods of Montello and Selva, northern Italy.

Oidium griseum is one of the very few species of the genus that appears

[4] The writer wishes to express his indebtedness to Mr. E. W. Mason of the Imperial Mycological Institute, Kew, England, for his kindness in furnishing this culture, as well as for other help received through correspondence.

to be parasitic either on a phanerogamic host or on another fungus. Because of this, it seems quite probable that, as Saccardo (Syll. Fung. **4**: 93. 1886) has noted, this species belongs in the genus *Ovularia*, although the shape and size of the spores, and the conspicuous sporogenous teeth, would apparently place the species here. A restudy of the type specimen is most desirable. The description is translated from the original.

11. OIDIUM AUREUM Link, Obs. in Ord. **1**: 18. *fig. 29.* 1809; Fries, Syst. Myc. **3**: 429. 1829.

Alysidium fulvum Kunze & Schmidt, Myk. Hefte **1**: 11. *pl. 1, fig. 6.* 1817.
Acrosporium fulvum (Kze. & Schm.) Persoon, Myc. Eur. **1**: 24. 1822.
Acrosporium aureum (Lk.) Persoon, Myc. Eur. **1**: 25. 1822.
Oidium fulvum (Kze. & Schm.) Link, in Linnaeus, Sp. Pl. ed. IV. **6**: 121. 1824; Fries, Syst. Myc. **3**: 430. 1829.
Torula aurea (Lk.) Corda, in Sturm, Deutschl. Fl. Abt. III. **1**(8): 79. *fig. 36.* 1829; Icon. Fung. **2**: 8. *fig. 35.* 1838.
Torula fulva (Kze. & Schm.) Corda, in Sturm, Deutschl. Fl. Abt. III **1**(8): 81. *fig. 37.* 1829.
Oospora aurea (Lk.) Wallroth, Fl. Crypt. Germ. **2**: 183. 1833.
?*Monilia Harknessi* Peck, N. Y. State Mus. Rept. **34**: 49. 1881.
?*Monilia platensis* Spegazzini, Anal. Mus. Nac. Buenos Aires, **8**: 86. 1902.
Oidium Murrilliae Sumstine, Mycologia **5**: 49. *pl. 82, fig. 6.* 1913.

Plate 4, Fig. A.

Colonies mostly effuse and closely but not densely hypochnoid, yellow when fresh, tawny or "Dark olive buff" when dry. The vegetative, mycelium is repent, 4.5–7μ in diameter, hyaline or nearly so, much branched and rather frequently anastomosing. Conidiophores erect or ascending, up to 200μ long, 7.5–9μ in diameter, few septate, hyaline except for some of the terminal spore-bearing cells that are distinctly yellowish under the microscope and which may be somewhat tapering or else slightly inflated, sparsely branched, the branches arcuate-ascending. Sporogenous teeth short, 2×1.5–3μ, or as hyaline scars. Conidia yellowish (19.8) — 23.5–25.5 $\times$ (10)–11–14.5μ, lemon-shaped and with an apiculus at either end or not infrequently with two apiculi at the outer end, one of which is obliquely attached, the conidia at the base of the chains are somewhat elongate and are truncate at the base, anastomoses between the conidia infrequent.

Specimen examined: GERMANY, Bergenlagen, Tamsel, Dec. 1, 1926, *P. Vogel* (FH).

Trichoderma aurea Persoon (Syn. Fung. p. 232. 1801) has often been cited by authors, even by Link himself, as the type of *Oidium aureum*, but there is little doubt that the fungus Link pictured is quite distinct from that figured by Persoon who later (l.c.) in making the combination of *Acrosporium aureum* definitely credits the species to Link and states that his *Trichoderma aurea* is quite distinct. It appears from Persoon's figure that he was correct, but that his fungus should be placed in *Penicillium*. For these reasons *Oidium aureum* is credited to Link in this paper. There is little doubt that *Alysidium fulvum* of Kunze and Schmidt is a synonym

of *O. aureum* for these authors state that "Es bildet anfangs goldgelbe, dann in das Rötliche überziehende, bey dem Trocknem aber wiederum verbleichende, . . ." colonies, and Corda (l.c.) in discussing *Torula fulva* states that they are morphologically alike although they differ in color, but this difference may well be explained by Kunze and Schmidt's statement quoted above. Apparently there has also been some confusion between this species and *O. hesperidicum* for Saccardo (Syll. Fung. **4**: 33. 1886) reduced his species to synonymy under *O. aureum*, but it seems from the single collection studied by the writer, that Saccardo's species is clearly distinguished by the color of the colony and by the closely aggregated or somewhat fasciculate conidiophores that give the colonies a tufted appearance. The specimen cited by Sumstine as *O. aureum* (Mycologia **5**: 48. 1913) produced smaller conidia than *O. aureum* and should be considered to be *O. ochraceum*. *O. Murrilliae*, described from Mexico appears to be a synonym of *O. aureum*, and is the only representative of the species that has been reported from the Western Hemisphere. The description furnished by Sumstine certainly agrees in all details with that made by the writer from the European material, but unfortunately the type specimen of the former was not available for study. *Monilia platensis* and *M. Harknessi*, as well as the additional species *M. effusa* Peck (N. Y. State Mus. Rept. **42**: 128. 1889) also were not available for study, but it seems more than likely that they may fall into synonymy under *O. aureum*.

12. OIDIUM ALBUM Sumstine, Mycologia **6**: 34. *pl. 116, fig. 1*, 1914.

Plate 2, Figs. E–F.

Colonies at first white but on drying become "Warm Buff," forming a thin floccose or hypochnoid layer. Conidiophores erect or suberect from repent, branched and intertwined vegetative mycelium, simple or once branched, 0–1–(2)—septate, mostly 50μ or less, occasionally up to 90μ in length, 6–9μ in diameter, isodiametric or the apical end somewhat inflated to 11μ and bluntly rounded. Vesicles absent. Denticles as prominent scars 3.6μ in diameter or occasionally as short, truncate prominences that are broader than they are long. Conidia hyaline or very light colored, 16–27$\times$12.5–14.5μ, ellipsoid or less frequently lemon-shaped, apiculate or truncate at the base and either with or without a terminal or oblique apiculus or both, in simple or branching chains, smooth or with very fine internal pitting on the inner surface of the endospore.

Specimen examined: NEW YORK, Bemus Point, on bark and on *Coriolus abietinus*, July 1913, *D. R. Sumstine*, **Type** (FH, CM).

In the dried condition, this species most closely resembles *O. aureum*, yet when it is seen under the microscope it may readily be distinguished by the shorter conidiophores, by the fact that the terminal cells of the conidiophores are not deeply colored, and by the conidia which are neither

so tapering nor so prominently bi-apiculate. The larger spores serve to segregate this species from *O. ochraceum.*

The writer is deeply indebted to Dr. David R. Sumstine for his kindness and generosity in furnishing a portion of the type specimen for study and for deposit in the Farlow Herbarium.

13. **Oidium ochraceum** (Povah) Linder n. comb.

Monilia ochracea Povah, Mich. Acad. Arts, Sci., Letters **13**: 181–182. *fig. 14.* 1931.

Plate 6, Figs. A–B.

Colonies when dry "Light orange yellow" or "Apricot yellow" to "Raw Sienna," effuse, pulverulent to rather densely hypochnoid. Vegetative mycelium is repent, septate, much branched and occasionally anastomosing. Conidiophores up to 360μ long (700μ acc. Povah), 5.5–7.5μ in diameter, erect, few septate, simple or the subterminal cell often bearing a single sharply ascending short branch. Sporogenous teeth short, cylindrical, truncate. Conidia light yellow to bright yellow in simple or branched chains, broadly lemon-shaped, (14.5)–16–20–(22) × (6)–9–11μ apiculate at both ends and not infrequently the outer end with two apiculi.

Specimens examined: CANADA, ONTARIO PROV., Lake Temagami, Aug. 19, 1935, *H. S. Jackson* (FH, TRT-8058); Lake Temagami, Sept. 9, 1935, *R. Bibbs* (FH, TRT-8050); North Parry Sound, Sept. 20–22, 1934, *H. S. Jackson* (FH, TRT-8052); UNITED STATES, MASSACHUSETTS, Hamilton, Oct. 5, 1940, *D. H. Linder* & *D. P. Rogers, 960* (FH, Rogers); OHIO, Seven Caves, Oct. 2, 1932, *W. B. Cooke, 1154* (FH, Cooke); IOWA, Iowa City, Aug. 31, 1936, *A. M.* & *D. P. Rogers* (FH); MICHIGAN, Rock River, Sept. 5, 1927, *A. H. Povah*, **Type** (MICH, FH); NEW JERSEY, Newfield, Oct. 1885, *J. B. Ellis*, as *Monilia aurea* Lk. in North American Flora, *1647*.

As has been pointed out above, this species differs from *O. aureum* by its smaller spores. It is possible that this species may be synonymous with *Monilia effusa* Pk. which has also been cited as being probably synonymous with *O. aurea*, but until it is possible to restudy Peck's type and to make additional measurements of the conidia, it is impossible accurately to to place his species. Should *O. effusum* prove to be the same as *O. ochraceum*, then the former would have priority.

14. **Oidium hesperidicum** (Sacc.) Linder n. comb.

Monilia hesperidica Saccardo, Michelia **1**: 87. 1877; Fungi Ital. **1**: *fig. 63.* 1877.

Plate 3, Figs. D–E.

Colonies composed of gregarious loose tufts, rubiginous. Conidiophores up to 200μ long, 5.5–9μ in diameter, hyaline or slightly colored, septate and somewhat constricted at the septa, erect or ascending, loosely branched and anastomosing frequently, the terminal cell somewhat inflated and rounded-tapering to the apical denticle. Sporogenous teeth few, one to rarely three, confined to the apical portion of the terminal cell and evident either as a scar or as a terminal apiculus, 1.8–4 × 3.5μ. Vesicles present as short, inflated, rounded-tapering branches or else as enlarged, 2-4-denticu-

late basal conidia. Conidia (18)–20–25–(28)×(9)–11–(14.4)μ at first hyaline but becoming fulvous with age, lemon-shaped or elongate ellipsoid and rounded-tapering towards either end where they are apiculate, occasionally obliquely or laterally denticulate, occasionally anastomosing with adjacent conidia or hyphae.

Specimen examined: ITALY, *P. A. Saccardo*, type distribution in Mycotheca Veneta, *1091* (FH).

Oidium hesperidicum is characterized by the rusty reddish-brown color of the colonies and by the fact that the colonies are constituted of an aggregation of relatively small tufts of conidiophores. Occasionally, and especially at the younger margins of the colony, the conidiophores are less likely to be fasciculate and the colony is more yellowish in color. In contrast to *O. aureum*, *O. hesperidicum* very rarely produces more than the single terminal sporogenous tooth.

15. **Oidium biforme** Linder sp. nov.

Plate 3, Fig. F.

Coloniae effusae, dense hypochnoideae vel breve gossypinae, "Burnt Sienna" marginibus "Light Ochraceous Buff;" conidiophoris generum duorum: 1) brevibus, rare usque 290μ longitudine, 8.5–12.5μ diametro, subhyalinis vel coloratis, rectis vel adscendentibus, ramosissimis et infra anastomosantibus, ramis arcuate-adscendentibus, cellulis terminalibus nonnihil inflatis et sporas sessilia gerentibus; 2) longioribus usque 500μ longitudine, 5.5–9μ diametro, simplicibus, rectis vel subrectis, fortiter fulvis coloratis; conidia 16–19×19–23μ, ellipsoideis, laevibus, basem apiculatis, subhyalinis vel fulvis, catenulatis.

Colonies effuse, densely hypochnoid to short-cottony, "Burnt Sienna," the margins "Light Ochraceous Buff." Conidiophores of two types: 1) short, occasionally up to 290μ long, 8.5–12.5μ in diameter, subhyaline to colored, erect or ascending, much branched, crowded and anastomosing below, the branches arcuate and ascending at a subacute angle, the terminal cells somewhat inflated and bearing chains of spores and 2) conidiophores up to 500μ long, 5.5–9μ in diameter, simple, erect or suberect, deeply fulvous colored and even or irregularly bullate along the length, slightly tapering towards the slender or inflated terminal cells of the conidiophores or the basal spore which may bear 1 to 3 chains of conidia. Conidia 16–19×19–23μ, smooth, subhyaline to deep yellowish brown, ellipsoid, conspicuously apiculate at the base and not at all or only slightly apiculate at the apex.

Specimens examined: CONNECTICUT, Woodbridge, Sept. 9, 1936, *J. R. Hansbrough* (FH, FP-69904); PENNSYLVANIA, Center Co., Buffalo Run, Nov. 13, 1936, *L. O. Overholts* (FH, Overholts-19816); NORTH CAROLINA, Cranberry, *R. Thaxter* (FH); TENNESSEE, Burbank, Aug. 20–Sept. 5, 1887, *R. Thaxter*, **Type** (FH-6701).

The striking character that separates this species from others that have been described in the genus is the existence of the long and short conidiophores, yet if the material is not carefully studied it may well be overlooked since the longer conidiophores are so much more conspicuous. Even without this character, however, the species, because of the morphology of the longer conidiophores and of the spores, can readily be distinguished. Interestingly enough, the short type of conidiophore interspersed among the longer and darker colored ones makes evident the relation between the group of species typified by *O. aureum* and that group which may be typified by *O. Curtisii*.

16. **Oidium aureo-fulvum** (Cke. & Ellis) Linder n. comb.

Monilia aureo-fulva Cooke & Ellis, Grevillea **8**: 12. 1886.

Plate 4, Fig. G.

Colonies effuse, hypochnoid, rust-colored or "Sanford's Brown" often with "Maize Yellow" margins. Conidiophores up to 300μ long, 5.4–9μ in diameter, ascending or suberect, subhyaline below, more deeply colored above and terminating in one or more deep golden brown terminal cells, or, as in the most mature conidiophores, all cells may be golden brown, loosely branched and sparingly anastomosing, the branches curved ascending, the septa distant. Sporogenous teeth evident only as slightly elevated scars on the conidiophores or as slight constructions at the end of the apical cells. True vesicles lacking. Conidia catenulate, readily falling apart, of two types: 1) subsphaerical or ellipsoid or broadly truncate-piriform, (13.5)–18–21.5–(22.5)×(10)–12–15.5–(16.5)μ and 2) irregularly flask-shaped with the apical end broadened and rounded, the basal somewhat elongate and cylindrical ending in a broad truncate base, 24.5–32.5×11.5–13.5μ; both types of spores are fuliginous.

Specimens examined: CANADA, ONTARIO PROV., London, Oct. 21, 1892, *J. Dearness, 2042* (FH); UNITED STATES, MASSACHUSETTS, Erving, Apr. 24, 1936, *G. D. Darker, 5621* (FH); Newton, Nov. 1892, *W. G. Farlow* (FH); Sharon, Sept. 1915; Oct. 10, 1922; May 1936, *A. P. D. Piguet* (FH); CONNECTICUT, North Bloomfield, Sept. 22, 1935, *H. G. Eno* (FH, FP-69377); Norwich, Nov. 1887, *W. A. Setchell* (FH); PENNSYLVANIA, Conneaut Park, July 16, 1906, *D. R. Sumstine* (FH); Westchester Co., Sept. 1879, *W. C. Stevenson*, **Type** (FH-Ellis); West Chester, Nov. 1879, *J. B. Gray* in Ellis, North American Fungi, *381* and in Rabenhorst, Fungi Europaei, *2685*, as *Oidium simile* (FH); GEORGIA, vicinity of Tallulah Falls, Ribbon Brook, Sept. 13, 1901, *A. B. Seymour* (FH); OHIO, Cincinnati, *C. G. Lloyd, 3925* (FH); MICHIGAN, Ann Arbor, Aug. 1921, *C. H. Kauffman* (FH, MICH); MISSOURI, Galloway, Oct. 28, 1933, *A. M. Rogers* (FH, Rogers); Walnut Grove, Oct. 29, 1933, *A. M. Rogers* (FH, Rogers-67); KANSAS, Rooks Co., Nov. 13, 1893, *E. Bartholomew* (FH).

In gross habit this species resembles *O. biforme* and *O. simile*. From the former it may be distinguished by the lack of the elongate conidiophores already mentioned in the discussion of that species. Under the hand lens the species occasionally cannot be separated from *O. simile*, although with the aid of the microscope the two can readily be told apart by their characteristic spores. A discussion of the confusion that has existed in the consideration of the two species will be found under *O. simile*.

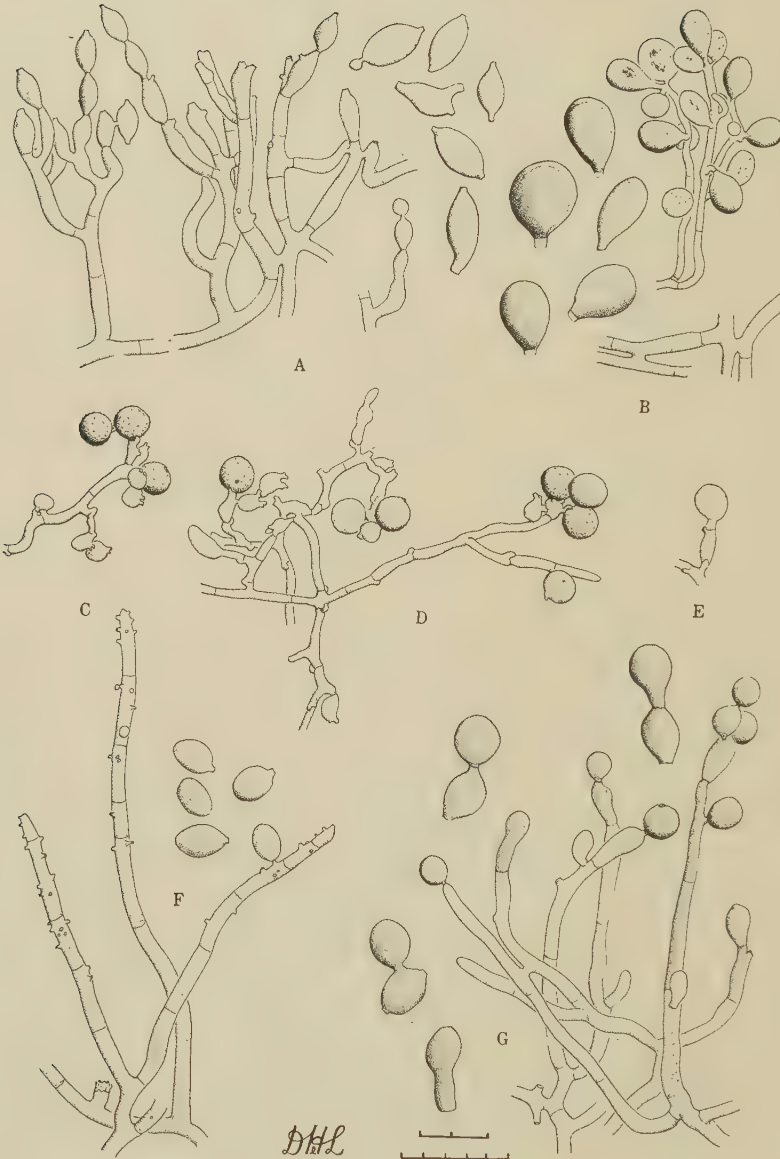

PLATE 4

FIG. A. *Oidium aureum* Corda. This species is characterized by its rather elongate, branched conidiophores, and the elongate, bi-apiculate conidia which are darker than all but the terminal or occasionally the subterminal cells of the conidiophores.

FIG. B. *Oidium simile* Berk. The large, thick-walled conidia that are borne on relatively short and slender conidiophores characterize this species. From co-type material in the Curtis Herbarium.

FIGS. C–E. *Oidium Morgani* Linder, showing the short conidiophores arising from the repent mycelium and immediately giving rise to a vesicle or a succession of vesicles that bear from one

17. **Oidium elongatum** Linder sp. nov.

Plate 6, Fig. H.

Coloniae fulvae vel "Sanford's Brown," pilosae; conidiophoris usque 1100μ longitudine, 9–11μ diametro, atro-fulvis, rectis, pauce lateraliter ramosis, ramulis brevibus, acute supinis; denticulis sporogenis inconspicuis, 3.5×1.5–5.5μ plerumque 1–5 ad apices cellularum ultimarum vel subultimarum; vesiculis ut cellulis brevibus inflatisque ad apices ramulorum; conidiis citriformibus, fulvis, laevibus, intus multi-guttulatis, 18–22×12.5–14.5μ, in catenulis ramosis.

Colonies rust-colored or "Sanford's Brown," pilose; vegetative mycelium repent, branched, septate, reddish-brown under the microscope. Conidiophores up to 1100μ long, 9–11μ in diameter, deeply colored, erect, with few lateral, sharply upcurved branches. Conidia lemon-shaped or irregularly lemon-shaped, light reddish brown under the microscope, smooth, in branching chains, 18–22×12.5–14.5μ, often filled with many guttulae that give the spores a granular appearance. Sporogenous teeth inconspicuous, 3.5×1.5–5.5μ, usually from one to five on the upper cells of the conidiophores and occurring near the apical septa. Vesicles usually modified short, inflated terminal cells of the conidiophores or their lateral branches, the upper lateral branches often becoming directly converted into vesicles.

Specimen examined: WYOMING, Cheyenne Mt., August 27, 1906, *W. C. Sturgis*, **Type** (NY, FH).

18. **Oidium rubiginosum** (FR.) Linder n. comb.

Sporotrichum rubiginosum Fries, Syst. Myc. **3**: 417. 1829.
Physospora rubiginosa Fries, Summa Veg. Scand. p. 495. 1849.
Physospora elegans Cavara, Rev. Myc. **11**: 182. *pl. 88 bis, fig. 4.* 1889.
Zygodesmus serbica Ranojevič, Ann. Myc. **8**: 397. *fig. 15.* 1910.
Rhinotrichum rubiginosum (Fr.) Sumstine, Mycologia **3**: 47. *pl. 37, fig. 1–2.* 1911.

Plate 2, Fig. C.

Colonies "Tawny" or rusty-brown, effuse, cottony or hypochnoid. Conidiophores up to 700μ long, 6–11.5μ in diameter, dilute fulvous to deep fulvous under the microscope, erect or ascending, frequently arcuate and anastomosing, the anastomoses between adjacent hyphae or between the apices of some hyphae and the sides of others. Vesicles pleurogenous or rarely acrogenous either sessile or borne on denticles of varying length, pear shaped to clavate and inflated, 13–36×9.5–15μ and bearing three to many denticles. Denticles 1.5–3×2–6.5μ, cylindrical or slightly expanded

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to four large colored, echinulate, globose spores. All septa are provided with clamp connections, including those at the base of the conidia. From type material.

FIG. F. *Oidium conspersum* (Lk.) Linder, distributed as *Rhinocladium olivaceum* Bres. in Jaap, Fungi Selecti Exsiccati, *296*.

FIG. G. *Oidium aureo-fulvum* (Cke. & Ellis) Linder. This species may be recognized by the pronounced coloration of the terminal cells of the conidiophores and by the flask-shaped as well as the ellipsoid to subglobose spores that are produced. Compare with *O. simile* above which has been confused with this species. From type material.

towards the base and produced on vesicles or pleurogenous, rarely acrogenous, on the conidiophores. Conidia ovoid to ellipsoid, less frequently subsphaerical, (13)–14.5–16–(17.5)×10.5–12.5–(15)μ, the content granular, the walls finely pitted so as to give the appearance of being minutely echinulate, fulvous to chestnut colored.

Specimens examined: ITALY, Padua, March 1878, *P. A. Saccardo* in Erb. Critt. Ital. Ser. II., *950* and Nov. 1880, *P. A. Saccardo* in Myc. Veneta, *1578* (both FH); SERBIA, Belgrade, Oct. 22, 1910, *N. Ranojevič* in Kabat & Bubak, Fungi Imperfecti Exsic., *690* as *Zygodesmus serbica* Ranoj. (FH, S-Sydow).

Although this species is not as yet known from North America, many specimens from the area have been labelled *Physospora rubiginosa* or *Rhinotrichum rubiginosum*. For the most part, such specimens should be placed either in *Oidium Curtisii* or in *Oidium ramosissimum*, although others may belong under *O. simile* or other species which are rusty-brown in color. The reason for the confusion is probably to be found in the fact that authentic Friesian examples are not available and the determinations accordingly have been the result of various interpretations of the original and not too specific description of Fries. The species as interpreted here is based on the specimens issued by Saccardo in the *Mycotheca Veneta* and the *Erb. Critt. Ital.* Nannfeldt, working at Uppsala, apparently had no Friesian material for comparison and illustrated the species with drawings of specimen 1578 of the Mycotheca Veneta which well may be chosen as the lectotype for the species. According to this concept, the outstanding character separating the species from others of the genus is the anastomoses of the conidiophores.

19. **Oidium ramosissimum** (B. & C.) Linder n. comb.

Rhinotrichum ramosissimum Berk. & Curt., Grevillea **3**: 108. 1875.

Plate 7, Figs. A–C.

Colonies "Ochraceous Buff," "Cinnamon Buff," "Sayal Brown," "Cinnamon Brown" to "Snuff Brown," densely velvety, densely to loosely hypochnoid. Conidiophores at first erect or ascending, much branched, frequently with age becoming prostrate from the many elongate branches, pellucid, dilutely colored, up to 425μ long, 6.5–12.5μ in diameter at the base, slightly tapering to 5μ at the apices but frequently inflated and expanded into bladder-like and proliferating branches or terminal cells, the sporogenous branches 17–23×10–15μ, ovoid to elongate-ellipsoid and often deciduous (vesicles), hyaline to light colored, bearing one to several sporogenous teeth. Sporogenous teeth conspicuous, cylindrical. Conidia smooth, subhyaline to dilutely colored under the microscope, ovoid to elongate-ovoid, lemon-shaped, or occasionally broadly ellipsoid, mostly bi-apiculate, 7.2–11×14.4–18μ.

Specimens examined: CANADA, ONTARIO PROV., Aurora, Oct. 1, 1931, *H. S. Jackson* (FH, TRT-3336); Hatchley, Aug. 27, 1934, *R. F. Cain* (FH, TRT-8063); New Durham, Sept. 4, 1934,

R. F. Cain (FH, TRT-3130, 3131); Norwich, Aug. 27, 1934, *R. F. Cain* (FH, TFT-8064); Round Lake, Oct. 17, 1914, *J. H. Faull* (MBG-44914); UNITED STATES, MAINE, York, Sept. 22, 1923, *R. Thaxter* (FH-6698); NEW HAMPSHIRE, Chocorua, Sept. 8, 1918, *W. G. Farlow* (FH); Cornish, Sept. 27, 1937, *H. G. Eno* (FH, FP-82223); VERMONT, North Hero, on roots of *Tsuga canadensis*, Sept. 13, 1936, *J. R. Hansbrough* (FH, FP-69245); Sharon, on *Robinia pseudoacacia*, Aug. 18, 1937, *T. J. Grant* (FH, FP-82007); MASSACHUSETTS, Arlington, *E. A. Burt* (FH-619); Cambridge, on underside of *Tilia* limb, Oct. 17, 1925, *A. P. D. Piguet* (FH); Canton, on moist decaying oak bark, Feb. 23, 1925, *D. H. Linder, 1027* (FH); Jamaica Plain, Oct. 12, 1922, *D. H. Linder, 113* (FH); Sharon, Nov. 17, 1934, *A.P.D. Piguet* (FH); CONNECTICUT, East Granby, Oct. 1, 1933 and July 24, 1937, *H. G. Eno* (FH, FP-63590, 81435); Whitneyville, June 21, 1937, *T. T. Ayers* (FH); NEW YORK, East Galway, on basswood, July 19, 1896, *E. A. Burt* (FH); Meyer's Point near Ithaca, Aug. 20, 1918, *J. R. Schramm* (MO-55496); North Greenbush, Nov. 25, 1915, *H. D. House* (NYS, MBG-14842); NEW JERSEY, Flemington, Aug. 3, 1935, *D. R. Sumstine;* Malaga, on oak railroad ties, Sept. 14, 1876, *Ellis* (FH-Ellis); Newfield, on pine railroad tie, Sept. 22, 1877, *J. B. Ellis* (FH-Ellis); Newfield, on *Sassafras* stump on ground, June 22, 1881, *J. B. Ellis* (NY-E); Newfield, on rotten cedar, Aug. 13, 1890, *J. B. Ellis* (FH-Ellis, NY-Ellis); PENNSYLVANIA, Bethlehem, June 28, 1883, *E. A. Rau* (BPI); West Chester, Oct. 1881, *Everhart, Haines, Jefferies* & *Gray* in Ellis, N. American Fungi, *825* (BM, FH); VIRGINIA, Radnor Heights, 1924, *C. L. Shear* (BPI); Richmond, on oak bark, Sept. 9 and 11, 1934, *D. H. Linder* & *R. F. Smart* (FH); SOUTH CAROLINA, Aiken, *H. W. Ravenel* in Ravenel, Fungi Americani Exsiccati, *576*, type distribution (BM-type, FH, MO); ALABAMA, Montgomery, Oct. 1916, *R. P. Burke, 232* (MO-57097); ILLINOIS, Riverside, Oct. 1903, *E. T.* & *S. A. Harper, 921* (FH); IOWA, Iowa City, Aug. 31, 1936, *A. M.* & *D. P. Rogers, 961* (Rogers).

O. ramosissimum is apparently the most common species in the region bounded on the west by the Mississippi River and extending from southern Canada to South Carolina, but when further collections are made it seems likely that it will be found to be as abundant in the West since it is not dependent on any one species of woody host, for it appears to demand only that the substratum be in the proper state of decay and in a suitable environment. The appearance of the colonies is such that the species may be confused with *O. Curtisii* from which it differs by its lemon-shaped or apiculate, ellipsoid, and smooth spores as contrasted with the spherical and finely internally roughened ones of *O. Curtisii*. In most instances, also, the very richly branched conidiophores furnish an additional character for the detection of this species.

20. **Oidium vesiculosum** Linder sp. nov.

Plate 6, Fig. G.

Coloniae "Deep Colonial Buff," effusae, arachnoidiae, nonnihil cristatae; conidiophoris usque 255μ longitudine, 7–10μ diametro, sursum leniter fastigatis, hyalinis, erectis vel adscendentibus, pauce ramosis, ramulis late adscendentibus, cellulis terminalibus frequenter tortuosis; denticulis sporogenis 2–3.5$\times$(2.5)–3.6–7.5μ, acrogenis vel ad partem apicalem cellularum pleurogenis; vesiculis hyalinis, subglobosis vel ovoideis, 14.5–23 $\times$10.5–14.5μ; conidiis 14.5–20$\times$10.5–11.5μ, ovoideis vel ellipsoideis, laevibus, hyalinis, breve catenulatis.

Colonies "Deep Colonial Buff," effuse, somewhat tufted or forming a thin arachnoid layer. Conidiophores up to 255μ long, 7–10μ in diameter, gradually tapering upwards, hyaline, erect or ascending from repent

PLATE 5

FIG. A. *Oidium effusum* (B. & C.) Linder. The abundant clamp connections, the globose conidia, and the numerous sporogenous teeth produced along the length of the conidiophore characterize this species.

FIGS. B–C. *Oidium armeniacum* (B. & C.) Linder is distinguished by the rough, globose conidia and the nodose-septate conidiophores, as well as by the incrustation of the conidia and conidiophores (Fig. C, ×—). From type material.

FIG. D. *Oidium sphaerosporum* Linder resembles *O. effusum* but lacks clamp connections and the conidiophores very rarely anastomose. From the type specimen.

mycelium, anastomosing below, few branched, the branches broadly ascending, the terminal cells slender and often zig-zag. Sporogenous teeth stout, conspicuous, 2–3.5 × (2.5)–3.6–7.5μ, mostly produced on the distal end of the cells of the upright conidiophores although occasionally on the repent mycelium. Vesicles present, mostly acrogenous, hyaline, subglobose to ovoid, 14.5–23 × 10.5–14.5μ. Conidia 14.5–20 × 10.5–11.5μ, ovoid to ellipsoid, smooth, hyaline, and in short chains.

Specimen examined: CHILE, Puntas Arenas, Magellanes, Jan. 1906. *R. Thaxter*, **Type** (FH).

Of the hyaline-spored species, this one most closely resembles *O. pulchrum* from Australia, but may be distinguished by the vesicles which although occasionally ellipsoid are predominantly globose or subglobose; by the slender apical and often zig-zag terminal cells; and by the apical position of the vesicles and conidia on the conidiophores.

21. **Oidium pulchrum** (Berk.) Linder n. comb.

Rhinotrichum pulchrum Berkeley, Journ. Linn. Soc. **13**: 175. *fig. 301.* 1873.

Plate 6, Fig. F.

Colonies effuse, hypochnoid, "Primuline Yellow." Conidiophores up to 400μ long, 6–9μ in diameter, hyaline to yellowish, suberect or ascending from the repent mycelium, loosely branched, the branches arising nearly at right-angles and curved, ascending, anastomoses frequent below, the terminal cell tapering upward and often bearing a sessile irregularly ellipsoid vesicle. Vesicles either as ellipsoid terminal cells or as short, conspicuously inflated lateral branches arising from any of the three upper cells of the conidiophores, with two to several sporogenous teeth. Sporogenous teeth conspicuous, 1.5–2.5 × 1.5–5.5μ, cylindrical, truncate. Conidia ovoid to ellipsoid, yellowish under the microscope, (12.5)–14.5–18–(20) × (9)–11–12.5μ, apiculate at the base, occasionally also at the apex.

Specimens examined: AUSTRALIA, Wangarette, in herb. Berkeley, **Type** (BM, K); Adelaide, National Park, 1914, *W. N. Cheesman* (K).

22. **Oidium gracile** Linder sp. nov.

Plate 6, Figs. C–E.

Coloniae effusae, velutinae, "Cream Color" vel "Naples Yellow;" conidiophoris usque 1000μ longitudine, 3.5–6.5μ diametro, hyalinis, erectis vel adscendentibus, laxe furcato-ramosis, ramulis arcuato-adscendentibus; denticulis sporogenis tenuibus, cylindricis, 0.5 × 1.5–3.6μ; vesiculis paucis, 1–5 conidia gerentibus; conidiis 12.5–16.5 × 9–12.5μ, ovoideo-ellipsoideis, laevibus, hyalinis.

Colonies effuse, velvety or short-cottony, "Cream Color" or "Naples

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FIG. E. *Oidium tomentosum* (B. & C.) Linder may be recognized by the elongate mostly simple conidiophores that become more deeply colored towards the apex. From the Bahama Island specimen.

Yellow." Conidiophores up to 1000μ long, 3.5–6.5μ in diameter, hyaline, erect or ascending, loosely sympodially or subdichotomously branched, not or rarely anastomosing, branches distant, arcuate-ascending, the sporogenous teeth confined to the rounded tapering terminal cells or the three end cells. Vescicles few, bearing one to several conidia and usually evident as relatively short and somewhat inflated terminal cells which bear one to several conidia. Sporogenous teeth slender, cylindrical, 0.5$\times$1.5–3.6μ. Conidia 9–12.5$\times$12.5–16μ, ovoid-ellipsoid, smooth, hyaline, frequently with a basal apiculus.

Specimens studied: GRENADA, B. W. I., Grand Etang, on *Euterpe* palm, *R. Thaxter* (FH); BRAZIL, Rio Grande do Sul, Sao Leopoldo, 1930, *J. Rick*, **Type** (FH); Sao Leopoldo, 1931, *J. Rick* (FH).

This species, with its elongate and subdichotomously branched conidiophores, is not likely to be confused with other members of the genus. It appears to be confined to the American tropics or subtropics where it grows on decaying wood, bark, and palm stems.

23. **Oidium chilense** Linder sp. nov.

Plate 2, Fig. A.

Coloniae effusae, tenaces, hypochnoideae, albae, canentes vel "Marguerite Yellow;" conidiophores usque 250μ longitudine, 8–11μ diametro, hyalinis, rectis vel assurgentibus, primo simplicibus demum pauce ramosis, ramis subrectangulariter oriundis lateque adscentibus, cellulis terminalibus subvesiculosis septoque constrictis; denticulis absunt vel ut cicatrices evidentibus; conidiis breve catenulatis, ovoideis vel ellipsoideis, 14.5–16.5–(18)$\times$(9)–10–(12)μ, laevibus, nonnumquam basim leviter truncato-apiculatis.

Colonies effuse, sparse, hypochnoid, whitish, cinereous or "Marguerite Yellow." Conidiophores up to 250μ long, 8–11μ in diameter, hyaline erect or ascending, at first simple and then few-branched, the branches arising nearly at right angles and broadly ascending, the lower branches often longer than the main axis and spreading horizontally, conspicuously constricted at the terminal septa, the terminal cells subvesiculose and bearing conidia. Denticles short or represented by slightly raised scars. Conidia sessile or subsessile, short-catenulate, 14.5–16.5–(18)$\times$(9)–10–(12)μ, smooth, hyaline, ovoid to ellipsoid, occasionally slightly truncate-apiculate at the base.

Specimen examined: CHILE, Puntas Arenas, Magellanes, Mar. 1906, *R. Thaxter*, **Type** (FH).

Oidium chilense shows a marked resemblance to *O. candicans* but this latter species produces considerably longer and proportionately more slender conidiophores and the conidia are produced on more prominent sporogenous teeth. Macroscopically, the colonies are very thin and hypochnoid whereas those of *O. candicans* are much better developed.

24. **Oidium Bloxami** (B. & Br.) Linder n. comb.

Rhinotrichum Bloxami Berkeley & Broome, Ann. Nat. Hist. 2nd Ser. **7**: 177. *pl. 7, fig. 19.* 1851.

Plate 2, Fig. B.

Colonies effuse, loosely hypochnoid, "Cinnamon Buff," "Chamois" to "Deep Colonial Buff." Conidiophores up to 255μ long, (7.2)–9–12μ in diameter, hyaline to dilutely colored, erect or suberect, somewhat crowded, anastomosing below, branches few and those coming off approximately at right-angles, ascending, not conspicuously constricted at the septa, usually terminated by an apical spore. Vesicles few, pleurogenous, globose to subglobose, with two to several sporogenous teeth. Sporogenous teeth or denticles short, broader than long, 2μ in diameter and varying from mere scars to 1.5μ in length, rarely longer, usually confined to the apical portions of one to three of the terminal cells, but occasionally on the lower cells. Conidia 14.5–16.5 $\times$ 9–11μ, ovoid to ellipsoid and often minutely apiculate, hyaline to light colored, the walls externally smooth but internally shallowly and minutely pitted to give the spores a granular appearance.

Specimen examined: ENGLAND, Twycroft, 1850, *Rev. A. Bloxam*, **Type** (BM).

25. **Oidium Morgani** Linder n. nom.

Physospora elegans Morgan, Cinci. Soc. Nat. Hist. Journ. **18**: 44–45. *pl. 3, fig. 23.* 1895, nec Cavara, Rev. Myc. **11**: 182. 1889.
Coniophora elegans (Morgan) v. Hoehnel, Ber. Deutsch. Bot. Ges. **37**: 155. 1919.

Plate 4, Figs. C–E.

Colonies pulverulent, "Ochraceous Buff," effuse. Sterile mycelium repent, lightly colored, much branched, nodose-septate, 5–7μ in diameter. Conidiophores up to 70μ long, arising from the repent mycelium, nodose septate, 5–7μ in diameter and not much differentiated from the sterile mycelium. Vesicles produced terminally or laterally, singly or in short chains and always subtended by a clamp connection. Conidia globose, 18–20μ in diameter, strongly colored, smooth to minutely tuberculose roughened, in short chains with each spore connected by a clamp connection. Sporogenous teeth 2.5 $\times$ 2–5.5μ, the terminal end with a lateral projection representing part of a clamp connection.

Specimen examined: OHIO, Preston?, on decaying wood, Mar. 8, 1892, *A. P. Morgan*, **Type** (FH, IA).

Of all the species in the genus *Oidium*, this one is the most remarkable and seemingly the most specialized because of the number of clamp connections present in the thallus where nearly every septum is provided with this structure which leaves little doubt as to the relationship of this imperfect phase to some basidial form. It is because of the clamp connections and the proportionately large size of the spores that the place of the species in this genus is obscured, yet if the morphology is studied it will be found that the characteristic features of the genus—conspicuous denticles, vesicles, and

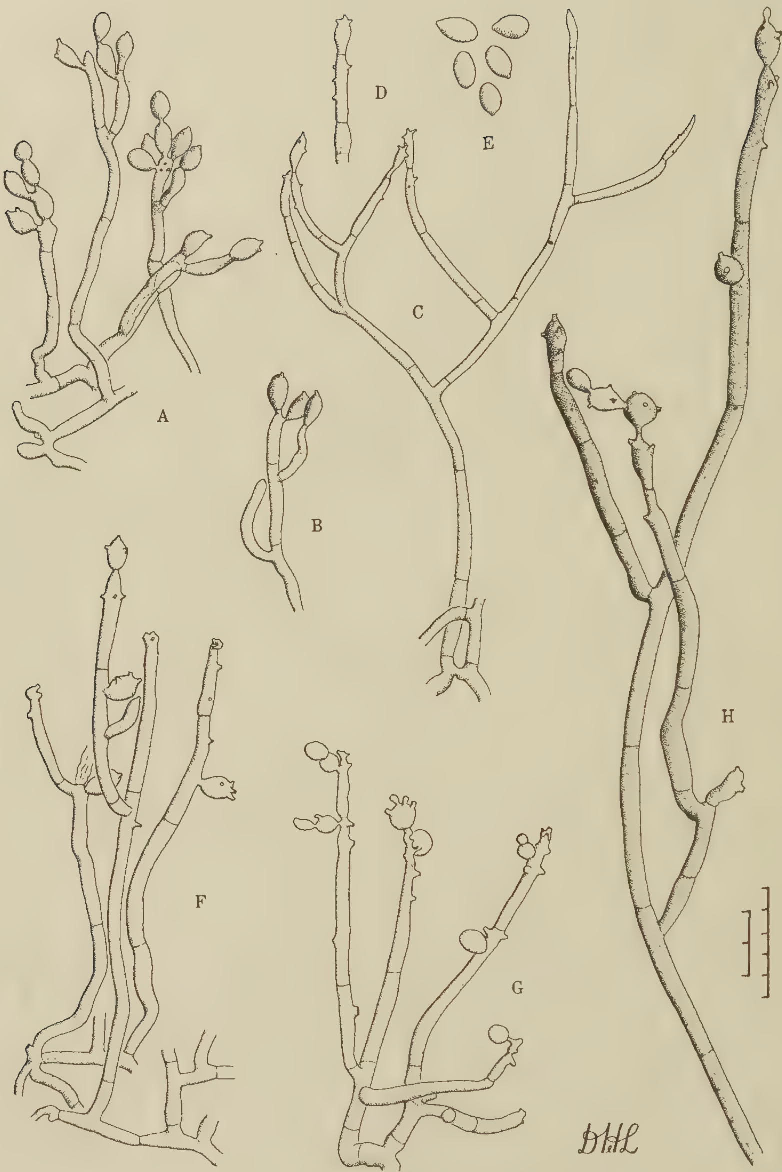

PLATE 6

FIGS. A–B. *Oidium ochraceum* (Povah) Linder. This species closely resembles *O. aureum* (pl. 4A) although separated by the more slender conidiophores and the smaller conidia. From the type material.

FIGS. C–E. *Oidium gracile* Linder is characterized by the subdichotomous branching of the slender conidiophores. The terminal cells may be inflated and vesiculoid as shown in Fig. D($\times$ 400). From type material.

FIG. F. *Oidium pulchrum* (Berk.) Linder, showing the sparsely ascending-branched conidiophores with relatively few sporogenous teeth and the more abundant vesicles. From type material.

the general habit of the fungus—are present even though in a somewhat modified form.

26. **Oidium armeniacum** (B. & C.) Linder n. comb.

Rhinotrichum armeniacum Berkeley & Curtis, Grevillea **3**: 108. 1875.

Plate 5, Figs. B–C.

Colonies effuse, hypochnoid, "Pale Orange Yellow" to "Capucine Orange." Conidiophores up to 250μ long, 5.5–7.5μ in diameter exclusive of the conspicuous crystalline incrustation, slightly tapering upwards, hyaline or yellowish, erect, ascending, or somewhat scandent, simple or rarely few branched below, even, septate and with clamp connections at the septa. Sporogenous teeth 1.5μ in diameter. 1.5–5.5μ long, cylindrical and apically truncate, straight or somewhat curved, simple or less frequently forked at the base, irregularly produced over the periphery of all but the lowermost cells of the conidiophores. Vesicles absent. Conidia globose or subglobose, (12.5)–14.5–(16.5)μ exclusive of the crystalline incrustation, occasionally (?) in short chains.

Specimen examined: SOUTH CAROLINA, on old fruiting body of *Polyporus Schweinitzii*, *H. W. Ravenel, 1086*, **Type** (BM, FH, K).

This species is definitely set off from all others of the genus by its incrusted globose conidia, its heavily incrusted conidiophores, and by the presence of clamp connections at the septa. When the fungus is mounted in eosine-glycerine, the incrustations appear to be permanent, but they disappear when the specimen is mounted in lactophenol whereupon the prominent sporogenous teeth and the clamp connections at the septa become evident. The hyphae of the type specimen are not spinulose as stated by Sumstine,[5] but granulated as described by the original authors.

27. **Oidium effusum** (B. & C.) Linder n. comb.

Zygodesmus effusus Berkeley & Curtis, Grevillea **3**: 145. 1875.

Plate 5, Fig. A.

Colonies effuse, hypochnoid, yellowish to "Cream Buff" or "Clay Color." Conidiophores up to 350μ long, 5.5–7μ in diameter, gradually tapering upwards, hyaline to light colored, nearly smooth to densely and minutely warty-spinose, frequently septate and with clamp connections at the septa, sparsely branched and occasionally anastomosing. Sporogenous

[5] Sumstine, D. R., Mycologia **3**: 49. 1911.

FIG. G. *Oidium vesiculosum* Linder. The simple conidiophores bearing short, stout sporogenous teeth, the globose vesicles, and the more or less zig-zag terminal cells distinguish this species. From type material.

FIG. H. *Oidium elongatum* Linder is characterized by the elongate colored conidiophores which bear few sharply ascending branches and prominent sporogenous teeth and vesicles. From the type specimen.

teeth numerous on the upper two-thirds of the conidiophore, straight or curved, simple or furcate, 1–1.5×1.5–4μ. Conidia yellowish under the microscope, globose, 10.5–18μ in diameter, minutely and rather densely ornamented with short, blunt spines, occasionally in very fragile, short chains.

Specimens examined: SOUTH CAROLINA, *H. W. Ravenel* in Herb. Berkeley; *2598*, **Type** (K); GEORGIA, Valdota, on coniferous wood, Nov. 1935, *V. K. Charles* (BPI, FH); FLORIDA, Gainesville, Mar. 27, 1938, *W. A. Murrill, F-16127* (FH).

The appearance of this species is reminiscent of *O. conspersum* from which it differs in the spinulose conidiophores, the presence of clamp connections, and the globose spores. This species reminds one of *O. sphaerosporum* but differs from it by the presence of clamp connections.

28. **Oidium sphaerosporum** Linder sp. nov.

Plate 5, Fig. D.

Coloniae "Naples Yellow" vel "Antimony Yellow," effusae, hypochnoideae; conidiophoris usque 450μ longitudine, basem 7–9μ diametro, apicem 3.5–7.5μ, leniter sursum fastigatis, laevibus, hyalinis vel dilute luteis, septatis, raro anastomosantibus; denticulis sporogenis cylindricis, 1.5–2×0.75–5.5μ, pleurogenis vel minus frequenter acrogenis; conidiis globosis, (12.5)–14.5–16–(18)μ diametro, subluteis vel luteo-brunneis, minute et pauce echinulatis.

Colonies "Naples Yellow" or "Antimony Yellow," effuse, hypochnoid. Conidiophores erect or somewhat irregularly bent, up to 450μ long, 7–9μ in diameter at the base, 3.5–7.5μ at the apex, slightly tapering upwards, smooth, hyaline to light yellowish, septate and without clamp connections, occasionally anastomosing. Vesicles none. Sporogenous teeth slender, cylindrical, 1.5–2×0.75–5.5μ, mostly pleurogenous but less frequently acrogenous, scattered the length of the conidiophores. Conidia globose, (12.5)–14.5–16–(18)μ in diameter, yellowish to yellowish brown, minutely and sparsely echinulate.

Specimen examined: MEXICO, near Cuernavaca at 7000 ft. elev., Dec. 28, 1909, *W. A. & E. A. Murrill, 545*, **Type** (FH, NY).

Under the low power of the microscope, this species may easily be confused with *Oidium effusum*, but under the higher powers it can readily be distinguished by the lack of clamp connections at the septa and by the lack of echinulations on the conidiophores. In the dried condition, the colors of the colonies are also distinct, but because of the small number of collections representing the two species and also because of the range of colors exhibited by other species in the genus, it would be unwise to place too much reliance on this criterion for the separation of the two.

29. **Oidium laevisporum** (Cke.) Linder n. comb.

Zygodesmus laevisporus Cooke, Grevillea **6**: 139. 1878.
Rhinotrichum laevisporum (Cke.) Sumstine, Mycologia **3**: 49. *pl. 38, fig. 1–2*. 1911.

Plate 7, Fig. G.

Colonies effuse, hypochnoid to tomentose, ochraceous or "Ochraceous Tawny." Vegetative mycelium loosely interwoven, loosely attached to the substratum, hyaline, 5.4–9μ in diameter. Conidiophores somewhat spirally twisted, up to 376μ long, 7.2–9μ in diameter, distantly septate, hyaline to light colored, loosely branched, the branches arising nearly at right angles to the main axis and then sharply curved-ascending. Vesicles few, spore-like, ellipsoid, 16–18 × 10.5–12μ, attached to the conidiophores by a slender tooth, but occasionally by a stouter isthmus, provided with 1–3–(5) denticles. Sporogenous teeth mostly apical but occasionally a few occur on the ultimate or penultimate cells. Conidia globose, 10.5–14.5μ in diameter minutely echinulate, yellowish under the microscope, occasionally in short, fragile chains.

Specimens examined: FLORIDA, Gainesville, under side of Magnolia, *H. W. Ravenel*, in Herb., M. C. Cooke, #94, **Type** (K) and in Ravenel, Fungi Americani Exsiccati, *58* (FH); NORTH CAROLINA, Cullowhee, June–July, 1897, *R. Thaxter* (FH).

Sumstine has already pointed out that this species very closely resembles *O. Curtisii* from which it differs in the few spicules (denticles). It also differs in the lighter color of the colonies, as well as of the conidiophores, and in the type of branching which in this species is less spreading and more sharply ascending. In common with *O. Curtisii*, the spores are globose and minutely echinulate and the conidiophores are loosely spirally twisted.

30. **Oidium Curtisii** (Berk.) Linder n. comb.

Aspergillus laneus Schweinitz, Syn. Am. Bor. p. 282. 1832, nec *A. laneus* Lk.
Aspergillus Curtisii Berkeley, in Ravenel, Fungi Carolin. **4**: no. 83. 1855.
Rhinotrichum Curtisii Berk. in Curtis, M. A., Botany of North Carolina p. 129. 1867; Berkeley, Grevillea **3**: 108. 1875.
Rhinotrichum globiferum Berkeley & Broome, Jour. Linn. Soc. *14*: 101. *pl. 5, fig. 20.* 1875.
Physosopora spiralis Penzig & Saccardo, Icon. Fung. Javan. p. 99, *pl. 67, fig. 2.* 1904.
Rhinotrichum Sumstinei Peck, Torr. Bot. Bull Club *34*: 103. 1907.
Rhinotrichum subferruginosum Sumstine, Mycologia **3**: 47. *pl. 37, fig. 3–5.* 1911.
Hypochnus sub-zygodesmoides Rick, Broteria (XXX) **3**: 152. 1934.

Plate 7, Figs. E–F.

Colonies loosely to densely hypochnoid, when fresh "Honey Yellow" on drying becoming "Tawny," "Cinnamon Brown," or "Hazel," up to 1 mm. thick. Conidiophores at first erect or ascending or occasionally with age becoming prostrate and the branches become erect or ascending, the branches mostly alternate, arising nearly at right angles and then slowly ascending, lax, pellucid dilutely colored or brownish, 6.5–8.5–(11)μ, slightly tapering upwards to 5 to 5.5μ, frequently inflated at the sporogenous, apical cell. Vesicles terminal or pleurogenous on the three subterminal cells, ovoid or ellipsoid, 13–34 × (5.5)–6.5–10–(12)μ, usually with three or more denticles. Conidia globose to subglobose, subhyaline to dilute brownish, the endospore inconspicuously and minutely internally pitted or roughened or rarely smooth, (8.5)–10–12–(13.5) × (9.3)–10–13.5–(15)μ.

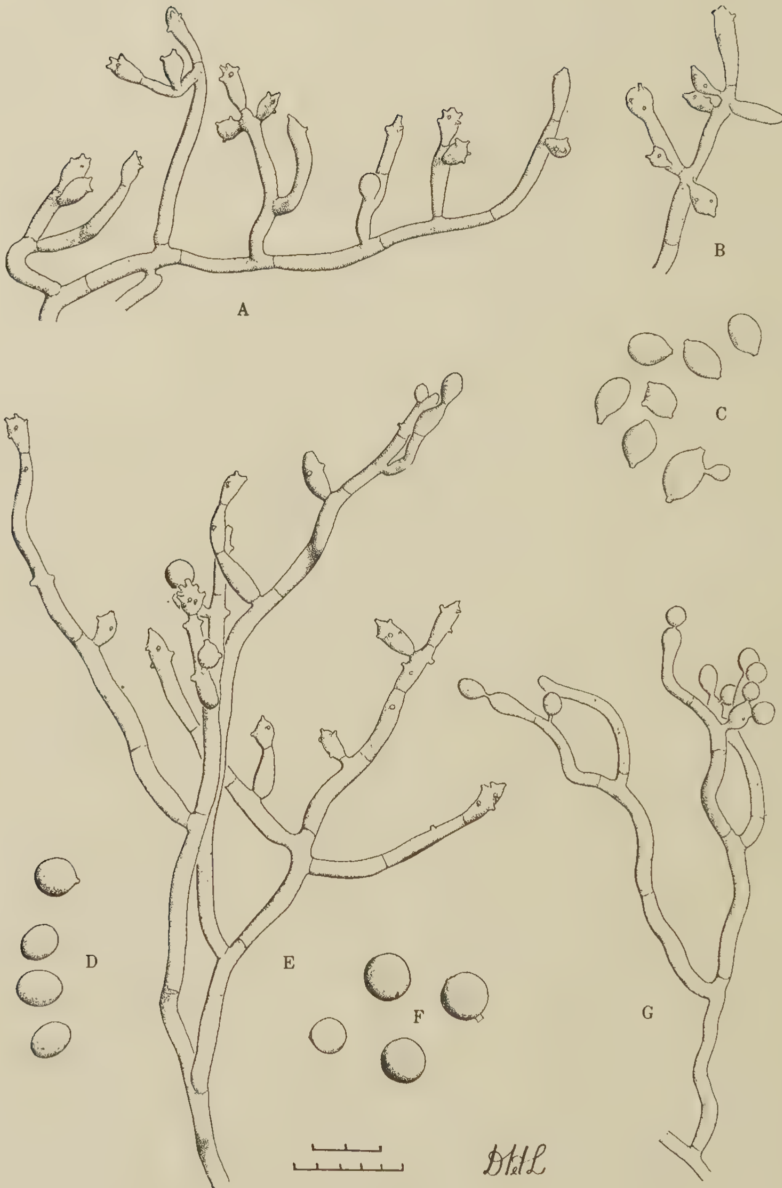

PLATE 7

FIGS. A–C. *Oidium ramosissimum* (B. & C.) Linder. The young conidiophores arise from the repent mycelium (A), but with age become more elongate and repeatedly branched (B) and bear numerous lemon-shaped spores (C) in chains.

FIG. D. *Oidium Curtisii* var. *ovalisporium* Linder. The spores of the variety tend to be more elongated than those of *O. Curtisii*. From the type specimen.

FIGS. E–F. *Oidium Curtisii* (Berk.) Linder. The spirally twisted, much branched, erect

Specimens examined: MASSACHUSETTS, Cambridge, July 10, 1941, *D. H. Linder* (FH); Cambridge, Aug. 1901, *A. P. D. Piguet* (FH); Newton, Oct. 1874, *W. G. Farlow* (FH); CONNECTICUT, Cheshire, June 28, 1889, *Thaxter & Seymour* (FH); East Granby, Sept. 23, 1933, *H. G. Eno* (FH, FP-81358); NEW YORK, Karner, Nov. 2, 1916, *H. D. House* (NYS, MO-54375); Vaughn's, on bark of *Ostrya* and on *Polyporus adustus*, *W. L. White* (FH); Vaughn's, Oct. 25, 1914, *S. H. Burnham, 9* (MO-44003); NEW JERSEY, Hasbrouck Heights, July 24, 1936, *A. P. D. Piguet* (FH); PENNSYLVANIA, Bethlehem, Oct. 1880 in Herb. Ellis, 3331 (FH-Ellis; NY); Fern Hollow, June 20, 1910, *D. R. Sumstine*, type of *Rhinotrichum Sumstinei* Pk. (NY); Olivet, July 13, 1931, *W. L. White* (FH); Philadelphia, on rotten pine wood, *J. W. Eckfeldt, 5* (FH, NY); West Chester, Aug. 1881, *Haines & Everhart* in Ellis, N. Amer. Fungi. *824* (BM, FH); NORTH CAROLINA, Cullowhee, June–July 1887, *R. Thaxter* (FH); SOUTH CAROLINA, without locality, *W. A. Carter, 586* (K); *H. W. Ravenel, 1765, 5025* (FH-Curtis); *H. W. Ravenel* as *Aspergillus Curtisii* Berk. in Ravenel: Fungi Carolin. Exsic., *83;* GEORGIA, Darien, Mar. 1881, *H. W. Ravenel* (BM); FLORIDA, Adams Key, on *Pogonomyces hydnoides*, Mar. 11, 1915, *K. J. Small & C. A. Mosier* in Exploration of the Florida Key: Tropical Florida, *5411* (NY); Coconut Grove, *R. Thaxter*, connected with *Pellicularia vaga* (B. & C.) Rogers (FH-6696, MO-43932); Daytona, on palmetto, *R. Thaxter* (FH); Eustis, Sept. 1897, *R. Thaxter* (FH, 7318); Gainesville, *H. W. Ravenel, 136* (BM); Grasmere, Mar. 1893, (NY); Palm Beach, *R. Thaxter* (FH); Plymouth, April 1893, in Herb. Ellis (NY); West Palm Beach, Mar. 18, 1939, *D. R. Sumstine* (FH); ALABAMA, Montgomery, *R. P. Burke, 196, 273* (MO-57072, 57157); OHIO, Chagrin Falls, Nov. 9, 1934, *R. W. Bingham, S-629* (FH); [Preston?] June 3, 1888, Feb. 17, 1888, May 11, 1887, *A. P. Morgan* (FH, IA); Sandusky, Aug. 10, 1904, *Kellerman* in Ohio Fungi, *195*; ILLINOIS, Bowmanville, Sept. 1899 (FH-Ellis); IOWA, East Okoboji, June 26, 1932, *G. W. Martin* (FH, IA); East Okoboji, Aug. 16, 1933, *A. M. & D. P. Rogers, 958* (FH, Rogers); Iowa City, Aug. 31, 1936, *A. M. & D. P. Rogers, 955*, connected with *Pellicularia vaga* (B. & C.) Rogers, (FH, Rogers); Turkey Creek, Aug. 17, 1934, *G. W. Martin* (FH, IA); MICHIGAN, Ann Arbor, Steinbach Woods, June 13, 1930, *L. E. Wehmeyer, 41* (FH, MICH); MISSOURI, Gray Summit, May 1931, on bark of *Quercus* sp., *D. H. Linder* (FH); Osage Highlands, Oct. 10, 1930, *D. H. Linder* (FH); Valley Park, Mar. 29, 1931, *D. H. Linder* (FH); Valley Park, Oct. 1931, *E. A. Burt* (MO-19419); KANSAS, Lawrence, Aug. 16, 1895, *M. A. Barber* (FH); SOUTH DAKOTA, *Williams* (FH-626); TEXAS, Houston, *C. Wright, 3892* (BM-Berkeley, FH-Curtis); BERMUDA, Paget Marsh, Mar. 26, 1922, *H. H. Whetzel* (CU); BAHAMAS, New Providence, Feb. 11, 1919, *L. J. K. Brace* (NY); JAMAICA, Hope, Oct. 25, 1902, *F. S. Earle, 93*, type of *Rhinotrichum su'ferruginosum* Sumstine (FH, NY); Moneague to Union Hill, *W. A. Murrill, 1167* (FH, NY); CUBA, San Blas, Trinidad Mts., June 20–21, 1941, *W. L. White* (FH); Soledad, June 19, 1941, July 8, 1941, *W. L. White, 301, 838* (FH); VIRGIN ISLANDS, St. Croix, Dec. 29, 1905, *C. Raunkiaer, 10* (FH); PUERTO RICO, Rio Piedras, June 1917, *J. A. Stevenson, 6543* (FH, NY); MEXICO, near Cuernavaca, 5000 ft. elev., Dec. 24–27, 1909, *W. A. & E. A. Murrill, 387* (FH, NY); Tecoman, Jan. 2, 1910, *W. A. & E. A. Murrill, 651, 678* (FH, NY); TRINIDAD, B. W. I., Four Roads Village, Aug. 14, 1923, *D. H. Linder, 46* (FH); VENEZUELA, *Fendler*, as *Rhinotrichum sphaerosporum* Berk. & Curt. (FH-Curtis); Caracas, 1903, *A. F. Blakeslee* (FH); BRITISH GUIANA, Bartica, Dec. 30, 1923, *D. H. Linder, 601* (FH); BRAZIL, Rio Grande do Sul, Sao Leopoldo, 1929, *J. Rick* (FH); Sao Leopoldo, 1931, *J. Rick*, type of *Hypochnus sub-zygodesmoides* Rick (FH); Santa Catharina, Sao Canisio do Porto Nova, 1928, *J. Rick, 75* (FH); Sao Paulo, Campinas, Mar. 2, 1941, *A. P. Viegas & A. S. Costa* (FH, Inst. Agron. Camp. 3698); ARGENTINE REPUBLIC, Buenos Aires, Mar. 1906, *R. Thaxter* (FH-6703); HAWAII, Palolo Valley, Mar. 20, 1911, *A. T. Speare, 4* (FH); CEYLON, *61*, type of *Rhinotrichum globiferum* Berk. & Br. (BM, K).

The connection between the conidial stage has been ascertained by following the hyphae from the conidiophores to the basidia. The relationship was first discovered by the writer while studying the specimen from Coco-

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conidiophores and the globose conidia, together with the many vesicles serve to distinguish this species.

FIG. G. *Oidium laevisporum* (Cke.) Linder. As in the preceding species, the conidiophores are spirally twisted but are lighter in color, more slender, and the branches are sharply curved-ascending. From type material.

nut Grove, Florida, that was collected by Professor Thaxter, and was found to be true in the material from Iowa that was collected by Dr. D. P. Rogers. Dr. Rogers has since substantiated this discovery in the same and additional material.

30a. **Oidium Curtisii** Berk. var. **ovalisporium** Linder var. nov.

Plate 7, Fig. D.

Similis est typo sed conidiis late ovoideis, $11.7–14.5 \times 12.5–16.5\mu$ raro globosis, laevibus vel endosporis minutissime asperulatis et conidiophoris non tortilibus.

Specimens examined: MADEIRA ISLANDS, 1910, *J. Barrets* in Torrend:—Fungi Sel. Exsic. *197* as *Monilia aurea* Lk. (FH); AFRICA, CAMEROONS, Sakbayeme, 1921, *Geo. Schwab* (FH); BELGIAN CONGO, Lulanga, Dec. 21, 1926, *D. H. Linder, 1745*, **Type** (FH); UGANDA, Entebbe, *Maitland, 198* (K).

The variety differs from the type species in the shape and size of the conidia and by the fact that the conidiophores are not spirally twisted. The very minute internal pittings or roughness of the endospore also relate this species to *O. rubiginosa*, but can be distinguished from it by the lighter colored spores, and the lighter conidiophores which are not arcuate-anastomosing. In color and consistency of the colony, this variety also resembles *O. ramosissimum* which, however, produces lemon-shaped or bi-apiculate conidia with smooth walls.

31. **Oidium tomentosum** (B. & C.) Linder n. comb.

Hymenochaete tomentosa Berkeley & Curtis, Linnean Soc. Journ. **10**: 335. 1868.
Trichosporium tomentosum (B. & C.) Patouillard, Myc. Soc. France Bull. **10**: 79. 1894.

Plate 5, Fig. E.

Colonies effuse, pilose, "Tawny" or "Ochraceous Tawny." Conidiophores up to 750μ long, $5.4–9\mu$ in diameter, slightly tapering upwards, hyaline or subhyaline near the base, the upper cells becoming more deeply colored, erect, mostly simple although occasionally with one or two short, arcuate-ascending branches from the terminal cells, frequently lateral anastomoses occur between adjacent conidiophores, septate, even or slightly constricted at the septa. Vesicles present as sessile or subsessile conidia which bear one or more chains of spores. Sporogenous teeth evident as plane or papillate scars 1.8μ in diameter. Conidia of two types: 1) globose, subhyaline to fulvous, in simple or branching chains, $(11.5)–12.5–14.5–(16)\mu$ in diameter, without or with one or more than one slender, short apiculus; 2) vesicle-like, piriform, truncate, produced acrogenously and often the basal cell of one or more than one fragile chain of conidia, $16–22 \times 10.5–14.5\mu$.

Specimens examined: BAHAMAS, Providence, on decaying pine, summer of 1904, *T. Barbour* (FH); CUBA, Central Soledad near Cienfugeos, rotted basal portion of *Bambusa vulgaris*, con-

nected with *Pellicularia lembospora* Rogers, July 8, 1941, *W. L. White, 824* (FH); Mina Carlota, Sierra de San Juan, Trinidad Mts. July 5, 1941, *W. L. White, 717* (FH); without locality, *C. Wright, 228*, **Type** (FH-Curtis).

The color of the colony of this species is somewhat like that of *O. aureo-fulvum* but from the latter species it is readily distinguished by its elongate, simple or sub-simple conidiophores and the globose and smaller conidia. In gross appearance this species also resembles *O. elongatum* but again the spherical spores as well as the morphology of the conidiophores readily separate the two.

It is interesting to note that the internal roughening of the endospore wall point to the relationship of this species to *O. Curtisii*, *O. rubiginosum*, and *O. conspersum*. Like *O. Curtisii* this species is connected with the basidiomycetous genus *Pellicularia*, and, as has been determined by tracing the mycelium from the conidiophores to the basidia, is the conidial stage of *P. lembospora* Rogers, sp. nov. ined.

EXCLUDED AND DOUBTFUL SPECIES

Because of the fact that the present paper was begun as a monograph of the genus *Rhinotrichum* and it was not discovered that the genus was untenable and must give way to *Oidium* until the war in Europe prevented the study of the type specimens of additional species of *Oidium*, this list must necessarily be incomplete. It may be said that in general, those forms occurring on the leaves of living plants and which represent the conidial phase of members of the Erysiphaceae are excluded from *Oidium* since they can not be considered congeneric with the type species of the genus. Sumstine (Mycologia **5**: 45–61. 1913) has already segregated, and quite properly, these and other species from the genus, and to his paper the reader is referred for additional data. In view of the fact that *Rhinotrichum* can not be maintained for those species that have been described under that name since 1837, it has seemed desirable to list here those that are excluded from both *Rhinotrichum* and *Oidium*, as well as those excluded from *Oidium*. The conclusions arrived at are based on the study of type material when the species name is followed by an exclamation point (!), on authentic material when followed by an asterisk (*), and on the writer's interpretation of the literature when neither of these signs are present.

1. OIDIUM CHARTARUM Link, as represented in Westendorp & Wallays, *Herb. Crypt. Belg.* no. *149* is certainly not *Oidium* but possibly a species of *Torula* sensu latu.

2. O. MEGALOSPORUM Berk. & Curt.(!) = *Sphaerosporium lignatile* Schw., 1834 = *Coccospora aurantiaca* Wallroth, 1833. Additional synonymy is furnished by Lindau in Rabenhorst, Krypt. Flora. 1^8: 14. 1904. Lindau questions the validity of this species as a fungus and would infer that the chlamydospores are the eggs of some animal. Such is not the case.

3. O. OBTUSUM Thuemen (*) is possibly a member of the heterogeneous genus *Sporotrichum* which as at present constituted has no limits.

4. RHINOTRICHUM ALBUM Petch = *Gonatorrhodiella coccorum* Petch. Petch (Trans. Brit. Myc. Soc. **16**: 61. 1931) reduced *R. album* to synonymy under *Gonatrorrhodiella*, where it could be placed only by extending the generic limits to a point where the genus would have no meaning. A study of *R. depauperatum* Charles, considered by the writer to be synonymous, shows that the spores are produced on reduced phialides which are arranged in whorls, the phialides being represented by stout teeth that, often in turn bear smaller teeth that give them a zig-zag appearance. Phialides with zig-zag apices characterize *Beauveria* and for this reason the new combination, **Beauveria coccorum** (Petch) Linder is proposed.

5. R. ASTEROIDES (Splendore) Verdun = *Sporotrichum asteroides* Splendore (cf. Dodge, C. W., Medical Mycology, p. 802. 1935).

6. R. AUREUM Cooke & Massee (!) = *Amblyosporium botrytis* Fresenius.

7. R. BEURMANNI (Matruchot & Ramond) Ota. For the present it seems advisable to return this species to *Sporotrichum* until that genus is more accurately defined. Dodge (l.c. p. 806) recognizes this organism as *Sporotrichum Schenkii* var. *Beurmanni* (Matr. & Ram.) Dodge.

8. R. BREVE Berk. & Curt. (!). The type specimen is in poor condition for study. The most that can be said is that the species can not be considered to belong in *Oidium*.

9. R. CANESCENS Speg. (*) and R. CANCESCENS var. SPECIOSCULUM Speg. (*) are definitely not species of *Oidium* and could more properly be placed in *Sporotrichum*, where they may be considered as one species which is parasitic on *Cercospora* spp.

10. R. CARNEUM Ellis & Everhart (!) belongs in the genus *Phymatotrichum* and is possibly synonymous with *Botrytis carneum* Schum.

11. R. CARTERI Cooke (!). The type specimen is in very poor condition and could not be studied sufficiently to determine the position of the species.

12. R. CHRYSOSPERMUM Sacc. (*) = *Didymotrichum chrysospermum* (Sacc.) Hoehnel.

13. R. CORTICIOIDES Cooke (!) = *Coniophora olivacea* (Fr.) Karsten. sensu Burt.

14. R. DECIPIENS Cooke (!). A basidiomycetous species.

15. R. DECOLORANS Cooke (!). The small, echinulate and catenulate spores that agree with Cooke's description and were found in the type specimen belong either to a species of *Aspergillus* or *Penicillium*.

16. R. DEPAUPERATUM Charles (!) = *Beauveria coccospora* (Petch) Linder. A discussion of this species is to be found under *R. album* Petch.

17. R. DOLIOLUM Pound & Clements. The type of this species is apparently lost, but from the description it does not seem to belong in *Oidium*.

18. R. FUSIFERUM Berk. & Curt. (!) = **Didymotrichum fusiferum** (B. & C.) Linder n. comb.

19. R. GOSSYPINUM Speg. (*). The specimen issued in Spegazzini's Fungi Guaranitici no. 77 appears to be synonymous with *R. canescens* Speg.

20. R. HERBICOLUM Ellis & Dearness. The type of this species has not been available for study. From the description it is impossible to place the species accurately although there is a possibility of it being synonymous with *O. Curtisii* (Berk.) Linder or it may even be a species of *Phymatotrichum*.

21. R. MICROSPORUM Berk. (!). The type specimen is badly fragmented and is unsatisfactory for study.

22. R. MINUTUM Saccardo (*) is definitely not a member of the genus *Oidium* and would be better placed in *Chloridium*, a genus which needs further study.

23. R. MURICATUM Ellis & Everhart (!) is a basidiomycetous species belonging in *Tomentella*.

24. R. OBLONGISPORUM Preuss is known only from the original description which, however, is insufficient to place the species accurately in *Oidium* where it obviously belongs. Those specimens that have been studied which were labelled *R. oblongisporum* have proved to be *Oidium conspersum* (Lk.) Linder.

25. R. OPUNTIA Berk. & Broome (!) belongs in the genus *Phymatotrichum*.

26. R. PARVISPORUM Petch appears to be synonymous with *R. album*, which see.

27. R. PSILONIOIDES Preuss is definitely not a species of *Oidium* and for the present may be known as *Periconia psilonioides* (Preuss) Sacc.

28. R. SCHENKII (Hektoen & Perkins) Ota is doubtfully distinct from its variety *Sporotrichum Schenkii* var. *Beurmanni* (q.v.). Dodge (Medical Mycology p. 806. 1935) recognizes this species as *Sporotrichum Schenkii* Hektoen & Perkins.

29. R. THWAITESII Berk. & Broome (!) = *Botrytis splendida* (Schw.) Sacc.

Soil Acidity in Relation to Alkaloid and Cyanogenetic Glucoside Production

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It has been demonstrated that the amounts of alkaloids and cyanogenetic glucosides produced in plants are generally greater when the concentration of electrolytes in their expressed saps is greater (McNair, 1941). The amounts of these substances are also increased by nitrogenous fertilizers. Much of the active nitrogen in alkaloids is in the amino form and consequently ammoniacal fertilizers may have a greater influence on alkaloid production than nitrate fertilizers. The rate of absorption and utilization of nitrates and ammonium salts by plant roots is markedly influenced by the *p*H value of the medium in which the roots are growing. Therefore, a study of the soil *p*H may produce some illuminating information on the formation of plant alkaloids and cyanogenetic glucosides.

INFLUENCE OF *p*H ON NITROGEN ABSORPTION

Pirschle (1929) was one of the first to show that in a pronounced acid medium plants can not obtain sufficient nitrogen from ammonium salts. In 1931 he noted that plants tolerate a much wider *p*H range for the utilization of nitrates than for ammonium salts and that with neither compound is there a single *p*H value at which all plants make their optimum growth. Tiedjens and Robbins (1931) observed that although seedling trees of peach and apple could absorb and assimilate ammonium salts over a wide *p*H range, they did not assimilate a sufficient amount of nitrogen for maximum growth unless the culture solution had a *p*H value of 7.0 to 8.0. Naftel (1931) noticed that the absorption of NH_4 by the cotton plant increased as the acidity of the culture solution decreased, while the absorption of NO_3 was only slightly affected by the reaction of the medium. The observation that plants absorb nitrogen in the form of ammonium salts more rapidly from the nutrient medium at a relatively high *p*H, while the nitrogen in the form of nitrates is absorbed more rapidly at a lower *p*H value, has been reported also by Addoms and Mounce (1932) for young cranberry plants; by Tiedjens and Blake (1932) for apple trees; by Clark (1933) for strawberry plants; by Davidson and Shive (1934) for peach trees; and by Tiedjens (1934) for tomato, cotton and the seedling plants of several varieties of apple.

Conrad (1934) considered that a plant absorbs the NO_3 ion more rapidly from a more acid medium because it can secure more easily therefrom the the requisite hydrogen ions to accompany the NO_3 ions into the plant. The same reasoning is applied for the absorption of the NH_4 ions from the more alkaline solutions. When both ions are present in approximately equal con-

centrations in neutral solutions more NH_4 ions will be absorbed because less energy is required to incorporate the nitrogen of the NH_4 ions into protein than in the case of the NO_3 ions. Also, it is quite likely that the nitrogen of the NH_4 ions could be incorporated into the structure of alkaloids more easily than that of the nitrogen of the NO_3 ions.

However, as Beaumont and Moore (1933) point out, the relative value of nitrates and ammonium salts in plant nutrition depends upon other factors besides *p*H. Among these factors are: age of the plants, kind of plant, concentration of medium, light, and the presence of other ions. Of these the two most important are (Miller, 1938) reaction of the medium and the age and kind of plant.

OCCURRENCE OF ALKALOIDS IN RELATION TO SOIL ACIDITY

A list of more than 334 species of plants arranged in accordance with their four reaction classes of soil habitats appears in Hortus (1941). This list, comprised of cryptogams, gymnosperms and angiosperms, was compiled by Wherry who characterizes the four soil types as follows:

Circumneutral (*p*H 8 to 6). Soils in which neither acid nor alkaline influences are markedly dominant. The soils of the Mediterranean region where so many of our garden plants are native are mostly of this class.

Minimacid (*p*H 7 to 6). Humus-rich meadows, swamps and woods, in calcareous regions. Fields and gardens under standard types of cultivation.

Subacid (*p*H 6 to 5). Many sorts of marshes, meadows, swamps and upland woods. Long-abandoned fields and gardens in non-calcareous regions.

Mediacid (*p*H 5 to 4). Various kinds of peat bogs. Swamps where the water is lacking in calcium bicarbonate. Thickets of rhododendron, kalmia and other ericaceous plants. Woods where such plants as hemlock, pine, spruce or oak are dominant. Accumulations of upland peat, rotting wood and similar material. Mountain peaks and sandhills where the substrata are non-calcareous.

The reactions given are considered to represent optimum values for the individual species, but many plants will grow nearly as well in soils of classes adjoining those in which the plant is listed.

In Relation to Genera.—Of the *p*H 8 to 6 group of plants comprising 100 genera, 15 genera (15 per cent) are known to contain alkaloids. Of the *p*H 7 to 6 group made up of 54 genera, 6 (11 per cent) are known to produce alkaloids. Of the *p*H 6 to 5 group of 129 genera, 14 (10.8 per cent) are known to form alkaloids. Of the *p*H 5 to 4 group of 51 genera, 2 (3.9 per cent) are known to make alkaloids (Table 1). With the decrease in *p*H values from *p*H 8 to 6 to *p*H 5 to 4, or in other words with the increase in soil acidity there is a definite decrease in the percentage of genera producing alkaloids.

In Relation to Families.—The occurrence of alkaloids in relation to the

soil-reaction of the genera of families can be determined. In the following, only the alkaloid with the maximum molecular weight will be given per genus as this is considered as representing the greatest effort on the part of the plant.

In the Compositae alkaloids are found in the *Dahlia* (trigonelline $C_7H_7O_2N$ mol. wt. 137, Henry) and in *Senecio* (senecifoline $C_{18}H_{27}NO_8$ mol. wt. 385, Henry). *Dahlia* is known to grow in soils with *p*H 8 to 6 and *Senecio* in *p*H 6 to 5.

In the Convolvulaceae alkaloids are found in *Convolvulus* (convolvidine

TABLE 1. *Occurrence of alkaloids and cyanogenetic glucosides in relation to soil acidity.*

Soil *p*H	Alkaloid genera	Cyanogenetic genera
Circumneutral soil plants 8–6	15/100 or 15%	17/100 or 17%
Minimacid soil plants 7–6	6/54 or 11%	12/54 or 22%
Subacid soil plants 6–5	14/129 or 10.8%	10/129 or 7.7%
Mediacid soil plants 5–4	2/51 or 3.9%	7/51 or 13.7%

$C_{32}H_{42}O_8N_2$ mol. wt. 578, Henry). *Convolvulus* is known to grow in soils with *p*H 8 to 6.

In the Crassulaceae an alkaloid has been found in *Sedum* (sedamine $C_{17}H_{24}NO_2$ mol. wt. 274, Kolesnikov and Shvartsman, 1939). *Sedum* grows at *p*H 6 to 5.

In the Gramineae an alkaloid is found in *Triticum* and *Avena*. This alkaloid is trigonelline ($C_7H_7NO_2$ mol. wt. 137, Wiesner). *Triticum* grows at *p*H 8 to 6 and *Avena* at *p*H 7 to 6.

In the Leguminosae alkaloids are found in *Pisum* (trigonelline $C_7H_7O_2N$ mol. wt. 137, Wiesner), in *Lotus* (cytisine $C_{11}H_{14}N_2O$ mol. wt. 190, Wiesner), in *Lupinus* (spathulatine $C_{33}H_{64}O_5N_4$ mol. wt. 596, Couch), in *Arachis* (arachine $C_5H_{14}N_2O$ mol. wt. 118, Wiesner), in *Baptisia* (cytisine $C_{11}H_{14}N_2O$ mol. wt. 190, Henry), in *Cytisus* (lupanine $C_{15}H_{24}ON_2$ mol. wt. 248, Henry), in *Ulex* ($C_{15}H_{20}O_5N_2$ mol. wt. 308, Henry). *Pisum* is known to grow in soils with *p*H 8 to 6, *Lotus* in *p*H 7 to 6, *Lupinus* in *p*H 7 to 6 and 6 to 5, *Arachis* in *p*H 6 to 5, *Baptisia* in *p*H 6 to 5, *Cytisus* in *p*H 6 to 5, and *Ulex* in *p*H 6 to 5. However, soil nitrogen as influenced by *p*H may not be as significant in the case of legumes as in other plants because the roots of most Leguminosae have tubercles containing bacteria (*Rhizobium* sp.). These plants with tubercles are able to take up much more atmospheric nitrogen.

In the Loganiaceae alkaloids are found in *Gelsemium* (kounidine $C_{21}H_{24}O_5N_2$ mol. wt. 384, Henry). *Gelsemium* grows at *p*H 6 to 5.

In the Lycopodiaceae alkaloids are found in *Lycopodium* (clavatoxine $C_{17}H_{27}O_2N$ mol. wt. 277, Henry). *Lycopodium* grows at *p*H 6 to 5.

In the Magnoliaceae alkaloids are found in *Magnolia* (magnolamine $C_{20}H_{23}NO_4$ mol. wt. 341, Proskurnina and Orekhov, 1938). *Magnolia* grows at *p*H 6 to 5.

In the Papaveraceae alkaloids are found in *Papaver* (narceine $C_{22}H_{27}O_8N$ mol. wt. 433, Henry), in *Adlumia* (homochelidonine $C_{21}H_{23}O_5N$ mol. wt. 369, Henry), in *Corydalis* ($C_{30}H_{26}O_5N_2$ mol. wt. 504, Henry), in *Dicentra* ($C_{37}H_{40}O_{11}N_2$ mol. wt. 688, Henry). *Papaver* grows at *p*H 8 to 6, *Adlumia* at 7 to 6, *Corydalis* at 6 to 5 and *Dicentra* at 6 to 5.

In the Ranunculaceae alkaloids have been found in *Delphinium* (staphisagroine $C_{40}H_{46}O_7N_2$ mol. wt. 666, Henry) and in *Coptis* (berberine $C_{20}H_{19}O_5N$ mol. wt. 353, Henry). *Delphinium* grows at *p*H 8 to 6 and 7 to 6, *Coptis* at *p*H 5 to 4.

In the Rhamnaceae an alkaloid has been found in *Ceanothus americanus* (Ceanothine $C_{29}H_{36}O_4N_4$ mol. wt. 504, Henry). *Ceanothus americanus* grows at *p*H 6 to 5.

In the Solanaceae alkaloids have been found in *Solanum* (solanine $C_{54}H_{98}O_{19}N_2$ mol. wt. 1078, Henry). *Solanum* grows at *p*H 6 to 5.

In the Symplocaceae an alkaloid has been obtained from *Symplocos* (harman = loturine $C_{12}H_{10}N_2$ mol. wt. 182, Henry). *Symplocos* grows at *p*H 7 to 6.

In the Taxaceae an alkaloid has been secured from *Taxus* (taxine $C_{37}H_{51}O_{10}N$ mol. wt. 669, Henry). *Taxus* grows at *p*H 8 to 6.

In the Umbelliferae an alkaloid has been analyzed from *Daucus* (daucine $C_{11}H_{18}N_2$ mol. wt. 178, Henry). *Daucus* grows at *p*H 8 to 6.

Some of the above compounds are found in more than one family, e.g., trigonelline ($C_7H_7O_2N$ mol. wt. 137) which is found in the Leguminosae, Moraceae, Gramineae, Solanaceae, Labiatae, Compositae, Apocynaceae, Rubiaceae and Dichapetalaceae. Berberine ($C_{20}H_{19}O_5N$ mol. wt. 353) is common to at least six families. Ranunculaceae, Berberidaceae, Papaveraceae, Menispermaceae, Anonaceae, Rutaceae all produce berberine or its derivatives or close allies. Harman ($C_{12}H_{10}N_2$ mol. wt. 182) is found in the Symplocaceae and in the Rubiaceae.

Consequently these three compounds are omitted from Table 2 as it is desired to use the more specific alkaloids.

From a study of Table 2 it is apparent that in the thirteen plant families considered which produce alkaloids there is in all instances a decrease in the maximum molecular weights of the alkaloids with a decrease in soil *p*H. The average maximum molecular weights of all such alkaloids in relation to soil *p*H is (*p*H 8 to 6) 504, (7 to 6) 469, (6 to 5) 471 and (5 to 4) 353.

In Relation to Hydrophytes and Halophytes.—In general hydrophytes live in an acid environment while halophytes are found in alkaline surroundings. Some specific experiments have determined the optimum *p*H's for several water plants. These are *p*H 3.4 for *Chlorella* (Wann and Hopkins,

1927); *Nelumbo lutea* 4.5 to 9.0 (Meyer, 1930) and *Lemna trisulca* 4.9 to 7.3 (Hicks, 1932). Of 338 angiosperm genera in which hydrophytes occur (Willis, 1931) only eight (2.3%) produce alkaloids, while of the 237 angiosperm genera which are known to contain halophytes (Uphof, 1941) nineteen (8%) form alkaloids.

SAP *p*H AND ALKALOID SYNTHESIS

In solving the problems of biosynthesis the chemist must find synthetic reactions which can take place in aqueous solution at the ordinary temperature and with the help of mild reagents only. Striking advances in this field are due to Schöpf of Darmstadt, who has studied the effect of varying the *p*H of the solution on the nature of the product and the yields in aldol condensations, Friedländer quinoline syntheses, the tropinone synthesis and related carbinol-amine condensations.

TABLE 2. *Relationship between the maximum molecular weights of alkaloids in genera and soil acidities (pH values).*

Family	Soil *p*H 8–6	Soil *p*H 7–6	Soil *p*H 6–5	Soil *p*H 5–4
Compositae			385	
Convolvulaceae	578			
Crassulaceae			274	
Leguminosae		569	308	
Loganiaceae			384	
Lycopodiaceae			277	
Magnoliaceae			341	
Papaveraceae	433	369	688	
Ranunculaceae	666			353
Rhamnaceae			504	
Solanaceae			1078	
Taxaceae	669			
Umbelliferae	178			
Average	504	469	471*	353

* Or 395 without the large molecular weight 1078 from the Solanaceae.

Schöpf and Lehmann (1932) found that 2-n-amyl-quinoline, which is one of the minor alkaloids of angostura bark (*Cusparia febrifuga* Humb., Rutaceae), could be directly obtained in 70 to 75 per cent yield by the condensation of o-aminobenzaldehyde with n-hexoylacetic acid at *p*H 7 to 9. This decarboxylation is remarkable and does not occur at *p*H 13.

The tropinone and pseudopelletierine syntheses also proceed directly at the appropriate *p*H, and the tables below show the yields of these bases obtained as the result of spontaneous decarboxylation. A citrate buffer was employed (Schöpf and Lehmann, 1935).

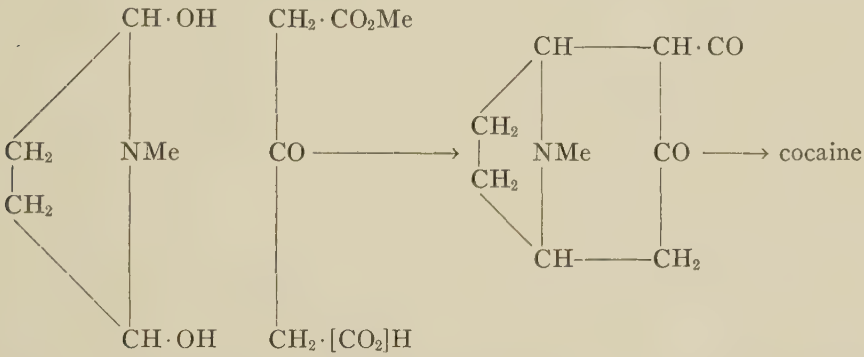
M/40 succindialdehyde, M/25 methylamine, M/25 (at *p*H 5, M/12) acetonedicarboxylic acid, M/10 buffer; 3 days; 20°.

*p*H	3	5	7	9	13
Yield of tropinone, %	38	90	73	70	3

M/80 glutardialdehyde, M/40 methylamine, M/40 acetonedicarboxylic acid, M/30 buffer; 8 days; 25°.

*p*H	3	5	7	9	11	13
Yield of pseudopelletierine, %	65	74	76	40	37	54

It may be significant that the optimum *p*H is a little on the acid side of neutrality, a condition satisfied by the cell sap of many plants. A further point is that the cocaine group of bases (to which tropinone belongs) probably arises from a protected acetonedicarboxylic acid and most plausibly from methyl hydrogen acetonedicarboxylate in view of the carbomethoxy- group occurring in the alkaloids.



In the pseudopelletierine (*Punica Granatum* L., Punicaceae) synthesis at *p*H 7 it was possible to raise the yield to 95 per cent of that theoretically possible by working in more concentrated solutions (M/12 of dialdehyde).

A further very interesting development was the synthesis of lobelanine (an alkaloid occurring in *Lobelia inflata* L., Campanulaceae) from glutardialdehyde, methylamine, and benzoylacetic acid at *p*H 4. The yield was 55 per cent, but was only 1 per cent at *p*H 2 and no product was obtained at *p*H 9. The base isolated was the naturally occurring cisisomeride.

Schöpf and Bayerle (1934) found that an aqueous solution of β—(3:4-dihydroxyphenyl)—ethylamine hydrobromide with acetaldehyde in slight excess at a *p*H 3 to 5 and temperature 25° gave an 83 per cent yield of 1—methyl—6:7—dihydroxy—1:2:3:4—tetrahydroisoquinoline hydrobromide, which only differs from the natural alkaloids carnegine (from *Carnegia gigantea* and *Cereus pecten aboriginum*, Cactaceae) 1:2—dimethyl—6:7—dimethoxy—1:2:3:4—tetrahydroisoquinoline) and salso-

line (*Salsola Richteri*, Chenopodiaceae) (1—methyl—6—hydroxy—7—methoxy—1:2:3:4 tetrahydroisoquinoline) in being unmethylated. It is interesting to note that both the artificially synthesized and the naturally occurring salsoline and carnegine are optically inactive.

The above experiments show five alkaloids similar to those found in some of the genera of six plant families. The genera and families are: Cactaceae, *Carnegia* and *Cereus;* Campanulaceae, *Lobelia;* Chenopodiaceae, *Salsola;* Erythroxylaceae, *Erythroxylum;* Punicaceae, *Punica;* and Rutaceae, *Cusparia*. These bases have been formed artificially at *pH* values such as those of soil in which plants live and also at *p*H values known to exist in some plant saps. However, the *p*H values for soil and sap of the particular plants which form these alkaloids are not known.

Some of these artificially synthesized alkaloids, e.g., tropinone and pseudopelletierine are formed over a wide range of *p*H values (*p*H 3 to 13), two others, lobelanine and carnegine have been made in acid solutions (viz., *p*H 2 to 4 and 3 to 5), while still another, the angostura bark base, has been made in the alkaline range *p*H 7 to 9. The maximum yields have been obtained at varying *p*H's between 5 and 9.

OCCURRENCE OF CYANOGENETIC GLUCOSIDES IN RELATION TO SOIL ACIDITY

In Relation to Genera.—Of the *p*H 8 to 6 group of plants comprising 100 genera, 17 genera (17 per cent) are known to produce HCN (Table 1). Of the *p*H 7 to 6 group of plants made up of 54 genera, 12 (22 per cent) are known to form HCN. Of the *p*H 6 to 5 group of 129 genera, 10 (7.7 per cent) are known to form HCN. Of the *p*H 5 to 4 group of 51 genera, 7 (13.7 per cent) are known to produce HCN. Therefore, with the decrease in *p*H there is an indicated decrease in the percentage of genera producing HCN.

In Relation to Families.—The occurrence of cyanogenetic glucosides in relation to the soil-reaction of the genera of families can be determined (Table 3). Of the 17 plant families considered which produce HCN there is a decrease in the total number of genera producing HCN with a decrease in the soil *p*H groups as follows: (*p*H 8 to 6) 17/46 or 37 per cent, (*p*H 7 to 6) 12/46 or 26 per cent, (*p*H 6 to 5) 10/46 or 21 per cent and (*p*H 5 to 4) 7/46 or 15 per cent.

In the Gramineae 2 (66 per cent) out of 3 genera that produce HCN live in soils with a *p*H of 6 or higher (i.e., 6 to 8). In the Leguminosae the relationship is 4 (80 per cent) out of 5 genera. In the Ranunculaceae 3 (75 per cent) out of 4, while in the Rosaceae the proportion is 8 (90 per cent) out of 9.

In Relation to Hydrophytes and Halophytes.—As shown above under alkaloid relationships, hydrophytes generally live in an acid environment

TABLE 3. *Relationship between cyanogenetic glucosides in genera and soil acidity* (*p*H *values*).

Family Genus	Occurrence of Cyanogenetic Compounds at *p*H 8–6	*p*H 7–6	*p*H 6–5	*p*H 5–4
Campanulaceae				
Campanula	HCN			
Campanula divaricata			HCN	
Compositae				
Centaurea out of 28 genera		HCN		
Convolvulaceae				
Convolvulus	O			
Ipomoea			HCN	
Cornaceae*				
Cornus florida		HCN		
Cornus canadensis				HCN
Crassulaceae				
Sedum			HCN	
Cruciferae				
Brassica	HCN			
Brassica		HCN		
Cardamine		HCN		
Iberis		O		
Dentaria			O	
Droseraceae				
Dionaea				HCN
Drosera				HCN
Ericaceae				
Erica out of 22 genera			HCN	
Gramineae				
Bromus	O			
Poa	HCN			
Secale	O			
Triticum	O			
Agrostis		O		
Avena		O		
Miscanthus		O		
Zea		HCN		
Agrostis			O	
Molinia				HCN
Leguminosae				
Lespedeza	O			
Medicago	HCN			
Melilotus	O			
Phaseolus	HCN			
Pisum	O			
Trifolium	HCN			
Wistaria	O			
Lotus		HCN		
Lupinus		O		
Phaseolus		HCN		
Stizolobium		O		
Vigna		O		

TABLE 3—*Continued*

Family Genus	Occurrence of Cyanogenetic Compounds at *p*H 8–6	*p*H 7–6	*p*H 6–5	*p*H 5–4
Arachis			O	
Baptisia			O	
Clitoria			O	
Cytisus			O	
Lupinus			O	
Ulex			O	
Linaceae				
Linum		HCN		
Onagraceae				
Oenothera	HCN			
Epilobium		O		
Fuchsia		O		
Oenothera glauca			HCN	
Papaveraceae				
Papaver	HCN			
Adlumia		O		
Corydalis			O	
Dicentra			HCN	
Polypodiaceae				
Adiantum	O			
Cheilanthes		O		
Athyrium			HCN	
Cheilanthes			O	
Dennstaedtia			O	
Dryopteris			O	
Pteridium			HCN	
Woodsia			O	
Asplenium				HCN
Polypodium				HCN
Woodwardia				O
Ranunculaceae				
Actaea	O			
Anemone	O			
Clematis	HCN			
Delphinium	O			
Paeonia	O			
Ranunculus	HCN			
Aquilegia		HCN		
Delphinium		O		
Cimicifuga			O	
Clematis			HCN	
Coptis				O
Rosaceae				
Cotoneaster	HCN			
Crataegus	HCN			
Malus	O			
Prunus	HCN			
Pyrus	HCN			
Rosa	O			
Spiraea	HCN			

TABLE 3—*Continued*

Family Genus	Occurrence of Cyanogenetic Compounds at pH 8–6	 pH 7–6	 pH 6–5	 pH 5–4
Amelanchier		HCN		
Filipendula		HCN		
Gillenia		O		
Prunus		HCN		
Rubus		O		
Aronia			O	
Dalibarda			O	
Rubus			O	
Potentilla				O
Rubus				O
Sorbus				HCN
Saxifragaceae				
Astilbe	HCN			
Deutzia	O			
Philadelphus	O			
Ribes	HCN			
Heuchera			O	
Hydrangea			HCN	
Mitella			O	
Parnassia			O	
Total	17/46 or 37%	12/46 or 26%	10/46 or 21%	7/46 or 15%

Authority for the presence of HCN in the above genera can be found in, Brunswik (1923), Foley and Musso (1925), Guerin (1929), Heilbronn (1929), Henry (1906), James (1939), Juillet and Zitti (1934), Mameli-Calvino (1923), Mirande (1913), Moran, Briese and Couch (1940), Petrie (1912), 1913, 1917, 1920), Rosenthaler (1919, 1922, 1926), Shearer (1938), and Steya (1937).

* According to Rosenthaler (1921) *Cornus* does not produce HCN.

while halophytes are found in alkaline surroundings. Of 338 angiosperm genera in which hydrophytes occur (Willis, 1931) only 10 (2.9 per cent) produce cyanogenetic glucosides, while of the 237 angiosperm genera which are known to contain halophytes (Uphof, 1941) 23 (9 per cent) form cyanogenetic glucosides.

pH and Cyanogenesis.—It has been known for a long time that mixtures of cyanogenetic plants and water that have been acidified or alkalized develop much less HCN than do mixtures that have not been so treated. Since in all of the cases studied cyanogenesis is the result of the hydrolysis of a nitrile glucoside by an enzyme it is to be expected that the reaction will proceed most rapidly at some particular pH value. Vulquin (1911) using buffer mixtures HCl, H_2SO_4 and Na_2CO_3 with amygdalin and emulsin, found that after an hour's reaction he obtained maximum yields of HCN at hydrogen ion concentrations between 0.2×10^{-5} and 0.6×10^{-5}

(or pH 5.69 to 5.22). Willstätter and Csányi (1921) report the optimum pH for the glucosidase action of emulsin or amygdalin as 6. Couch and Briese (1939) studied the effect of hydrogen ion concentration on cyanogenesis in sorghum. They used dried Johnson grass (*Andropogon halepensis*) and two varieties of sorghum (*Andropogon sorghum*) hegari and spur feterita. The pH ranges for the optimum production of HCN were for hegari (4.12 to 4.86), for spur feterita (4.10 to 4.86) and for Johnson grass (5.04 to 5.16).

The cyanogenetic glucoside amygdalin has been found in various members of the Rosaceae: *Amelanchier vulgaris*, *Cotoneaster vulgaris*, *Crataegus Oxycantha*, *Prunus amygdalus*, *P. laurocerasus*, *P. serotina* and *Pyrus Malus*. Members of all of these genera are known to grow in soil of pH 8 to 6.

The other cyanogenetic glucoside experimented with in regard to pH range and optimum HCN production is that of the Andropogons of the Gramineae. The soil pH for these Andropogon species may be similar to that of the closely related genus *Zea*. The pH for *Zea* which is known to form HCN is 7 to 6.

It is to be noted that the soil pH ranges for the above listed members of the Rosaceae and Gramineae are between 8 to 6, which are above that of the pH of optimum HCN production for their glucosides (Rosaceae 6 to 5.22, Gramineae 5.16 to 4.10).

In connection with cyanogenetic glucoside formation and decomposition it is of interest to know that Johannsen (1888) found emulsin and amygdalin in separate tissues in almond kernels. Emulsin, he found, was contained in the radicle and plumule, and in the vascular bundles of the cotyledons, while the parenchyma of the cotyledons contains the amygdalin.

SUMMARY

The amounts of alkaloids and cyanogenetic glucosides produced in plants are generally greater when the concentration of electrolytes in their expressed saps is greater. The amounts of these substances are increased by nitrogenous fertilizers. As much of the active nitrogen in alkaloids is in the amino form, NH_4 fertilizers may increase alkaloid production more than NO_3 fertilizers. The rate of utilization of NH_4 and NO_3 is greatly influenced by the pH value of the soil. This study is undertaken to develop some relationships between soil pH and alkaloid and cyanogenetic glucoside production.

Of the group of plants living on soils of pH 8 to 6 comprising 100 genera (15 per cent) are known to contain alkaloids. Of the pH 7 to 6 group made up of 54 genera, 6 (11 per cent) are known to produce alkaloids. Of the pH 6 to 5 group of 129 genera, 14 (10.8 per cent) are known to form alkaloids. Of the pH 5 to 4 group of 51 genera, 2 (3.9 per cent) are known to make

alkaloids. Therefore, with the decrease in *p*H there is a definite decrease in the percentage of genera producing alkaloids.

Of the thirteen plant families considered which produce alkaloids there is in all instances a decrease in the maximum molecular weights of the alkaloids with a decrease in soil *p*H. The average maximum molecular weights of all such alkaloids in relation to soil *p*H is (*p*H 8 to 6) 504, (7 to 6) 469, (6 to 5) 471 and (5 to 4) 353.

In general, hydrophytes live in an acid medium while halophytes are found in alkaline surroundings. Angiosperm genera in which hydrophytes are found produce fewer alkaloids and cyanogenetic glucosides than halophytic genera.

Five alkaloids similar to those found in the Cactaceae, Campanulaceae, Chenopodiaceae, Erythroxylaceae, Punicaceae and Rutaceae have been synthesized artificially at *p*H values such as those of soil in which plants live and also at *p*H values known to exist in some plant saps.

Of the *p*H 8 to 6 group of plants comprising 100 genera, 17 genera (17 per cent) are known to produce HCN. Of the *p*H 7 to 6 group of plants made up of 54 genera, 12 (22 per cent) are known to form HCN. Of the *p*H 6 to 5 group of 129 genera, 10 (7.7 per cent) are known to form HCN. Of the *p*H 5 to 4 group of 51 genera, 7 (13.7 per cent) are known to produce HCN. Therefore, with the decrease in *p*H there is an indicated decrease in the percentage of genera producing HCN.

Of the 17 plant families considered which produce HCN there is a decrease in the total number of genera producing HCN with a decrease in the soil *p*H groups as follows: (*p*H 8 to 6) 17 or 37 per cent, (7 to 6) 12 or 26 per cent, (6 to 5) 10 or 21 per cent, (5 to 4) 7 or 15 per cent.

In the Gramineae 2 (66 per cent) out of 3 genera that produce HCN live in soils with a *p*H of 6 or higher (i.e., 6 to 8). In the Leguminosae the relationship is 4 (80 per cent) out of 5 genera; in the Ranunculaceae 3 (75 per cent) out of 4, while in the Rosaceae the proportion is 8 (90 per cent) out of 9.

Optimum cyanogenesis occurs with amygdalin (Rosaceae) at *p*H 6 to 5.22, while optimum cyanogenesis occurs in the cyanogenetic glucoside(s) of *Andropogon* (Gramineae) at *p*H 5.16 to 4.10. The soil *p*H for such members of the Rosaceae and for *Zea*, a closely related HCN producing genus to *Andropogon*, is *p*H 8 to 6 which is above that of optimum glucoside decomposition.

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A Review of the Myrmecotherous Genus Tracheliodes (Hymenoptera: Sphecidae: Pemphilidini)

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A century ago Herrich-Schaeffer in an explanatory table to the subgenera of *Crabro*[1] included an unnamed new genus which was based on the new species he later described as *trochanteribus*[2] and referred somewhat doubtfully to *Ceratocolus*. Subsequently in 1845, Dahlbom used a closely related species, *Crabro Megerlei*,[3] as a basis for his monotypic new subgenus *Brachymerus*, the name of which, however, was unfortunately a homonym of Chevrolat's 1841 Erotylid genus. Cognizant of this Morawitz two decades later proposed *Tracheliodes*, according it subgeneric rank, and including therein four species[4] of which Ashmead in 1899 selected *Megerlei* as type, thus making *Brachymerus* absolutely synonymous with *Tracheliodes*. Finally in 1892, Pérez, probably unaware of either of these previous names, erected the new genus *Fertonius*, named in honour of Charles Ferton, the distinguished French biographer of these wasps, for the reception of *Crabro bucephalus* Smith, 1856 and *Crossocerus luteicollis* Lepeletier and Brullé, 1835, both of which are synonyms of *Crabro 5-notatus* Jurine, 1807, one of the two European species now assigned to *Tracheliodes*. Thus the name of Pérez must be recorded as a synonym of the much earlier one of Morawitz.

The first North American species referred to the present genus was *Tracheliodes mortuellus* Cockerell, a fossil from the Miocene shales at Florissant, Colorado. But no modern form was definitely recorded from the Nearctic Region until 1936 when the late Miss Grace A. Sandhouse characterized *Tracheliodes hicksi* from Boulder Canyon in Colorado. This, however, was not the first recent North American species of *Tracheliodes* described, for the Californian form, *Crabro foveolineatus*, which Viereck described in 1910 from Shasta County and incorrectly allocated to the subgenus *Cuphopterus*, is, as an examination of the type has revealed, clearly

[1] Fortsetzung von G. Panzers Fauna Ins. Germ., Heft 179, p. 5 (1841).

[2] This species is given as *trochantericus* in the key on p. 45 (Fn. Ins. Germ., Heft. 181), but in the description on p. 46 and elsewhere as *trochanteribus:* the latter, I believe, is the correct orthography. This point, however, is a minor matter, since in any event *Ceratocolus? trochanterib*/or/*cus* Herrich-Schaeffer, 1841 is a synonym of *Crabro 5-notatus* Jurine, 1807 [= *Tracheliodes 5-notatus* (Jur.)].

[3] *Crabro Megerlei* Dahlbom, 1845 is a synonym of *Crossocerus curvitarsus* Herrich-Schaeffer, 1840. The latter specific name is usually written "*curvitarsis*"; but Herrich-Schaeffer's original orthography was *curvitarsus*.

[4] The four specific names originally given by Morawitz as exponents of *Tracheliodes* were: *Ceratocolus trochantericus* H.-Sch. [1841 = *Crabro 5-notatus* Jurine, 1807]; *Crossocerus luteicollis* Lepel. & Br. [1835 = *Crabro 5-notatus* Jurine, 1807]; *Crossocerus curvitarsus* H.-Sch. [1840; a valid species]; and *Crabro* (*Brachymerus*) *Megerlei* Dahlbom [1845 = *Crossocerus curvitarsus* H.-Sch., 1840].

a member of the present genus. Additional unrecorded and undescribed Nearctic material of *Tracheliodes* is now before me, and I consequently present here a critique of this interesting myrmecotherous genus.

Tracheliodes A. Morawitz

Crabro [in part] Jurine, Nouv. méthod. class. Hymén., I, p. 212 (1807).—Van der Linden, Nouv. Mem. R. Acad. Sci., Bruxelles, V, p. 57, (1827).—F. Smith, Cat. Hymen. Brit. Mus. IV, p. 416 (1856).—Bingham, Faun. Brit. Ind., Hymen., I, p. 321, (1897).

Crabro (*Crossocerus*) Dahlbom, Hymen. Europ., I, p. 384 (1845). [In part, *nec* Lepeletier and Brullé.]

Crossocerus [in part] Lepeletier & Brullé, Ann. Soc. Ent. France, III, p. 769 (1835).—Herrich-Schaeffer, Faun. Insect. German., Fasc. 179, tab. 19 (1840).—Lepeletier, Hist. Nat. Insect., Hymén., I, 172 (1845).

Ceratocolus? Herrich-Schaeffer, Faun. Insect. German., Fasc. 181, tab. 14 (1841).

Crabro (*Brachymerus*) [*nec* Chevrolat, 1841], Dahlbom, Hymen. Europ., I, p. 525 (1845).—Kohl, Ann. K. K. Naturhist. Hofmus. Wien, XI, pp. 485, 487 (1896). Dalla Torre, Cat. Hymen., VIII, p. 579 (1897).

Crabro (*Tracheliodes*) A. Morawitz, Bull. Acad. Sci. St. Petersbourg, IX, p. 249 (1866).—Kohl, Ann. K. K. Naturhist. Hofmus. Wien, XXIX, p. 322 (1915).—Berland, Faune de France, X, p. 179 (1925).

Crabo (*Cuphopterus*) [in part, *nec* Morawitz] Viereck, Proc. Ent. Soc. Washington, XI, p. 44 (1909).

Brachymerus [*nec* Chevrolat, 1841] Ashmead, Canad. Entom., XXXI, p. 219 (1899).—Schmiedeknecht, Hymen. Mitteleurop., p. 182 (1907).

Fertonius Pérez [in Ferton], Act. Soc. Linn. Bordeaux, XLIV, p. 341 (1892).

Tracheliodes Cockerell, Bull. Mus. Comp. Zoöl., Harvard Coll., L, p. 45, (1906).—Schmiedeknecht, Hymen. N.-u. Mitteleurop., Zw. Aufl., p. 659 (1930).—Pate, Mem. Amer. Ent. Soc., no. 9, p. 66 (1937).

GENOTYPE: *Crabro* (*Brachymerus*) *Megerlei* Dahlbom, 1845 [=*Crossocerus curvitarsus* Herrich-Schaeffer, 1840 = *Tracheliodes curvitarsus* (Herrich-Schaeffer)]. (Designation of Ashmead, 1899, Canad. Entom., XXXI, p. 219.)

The tri-articulate labial and sexarticulate maxillary palpi, and the slender elongate fore trochanters differentiate *Tracheliodes* from all other Pemphilidine genera except the peculiar Neogaeic entity *Enoplolindenius*. But unlike the members of that genus, and the large majority of the remaining Pemphilidine wasps as well, the inner eye orbits of *Tracheliodes* are not strongly convergent toward the clypeus and antennal sockets; instead they are more or less parallel and thus cause the front to be quite broad below and the antennal sockets relatively remote from the lower inner orbits.

Generic Features.—Moderately small, semifulgid forms. Head subquadrate in anterior aspect, transversely subrectangular to subquadrate in dorsal aspect. Eyes usually with a very sparse microscopic puberulent pubescence; generally not much more appreciably coarsely facetted anteriorly than posteriorly; inner orbits subparallel to slightly convergent below, never strongly convergent toward clypeus and antennal sockets. Malar space wanting. Front relatively flat, broad, subquadrate to sub-

rectangular, without a distinct scapal basin. Vertex flat, horizontal, with supra-orbital foveae well developed in females but obsolescent or absent in males; ocelli moderately large, arranged in either a low or high triangle, the ocellocular distance always distinctly longer than the postocellar line; temples moderately well developed, ecarinate; occipital carina distinct but neither flanged, foveolate, a complete circle in extent, nor attaining the hypostomal carinule bordering the oral fossa. Antenna situated low on face on dorsal margin of clypeus, the antennal sockets subcontiguous to each other but relatively remote from nearest lower inner orbit, the antennocular distance at least twice the length of the interantennal line; thirteen-segmented in males and twelve-segmented in females; scapes relatively straight, more or less cylindrical, ecarinate; pedicel not longer than first flagellar article; flagellum simple, without excisions, teeth, or dilation of any sort in males. Clypeus transverse, short, median length about one-fourth the vertical eye length, flat or tumid discally, never keeled medially. Maxillary palpi with six, labial palpi with three segments. Mandibles stout, bidentate at apex in both sexes; lower margin entire. Females without a psammophore.

Thorax finely punctate and more or less aciculate. Pronotum short, transverse, situated on a level with the mesonotum, dorsal surface not transversely carinate anteriorly but posterior margin strongly impressed. Mesonotum simple; sutures between mesonotum and scutellum, and scutellum and postscutellum strongly impressed; axillae moderate, lateral edges never sharply margined; scutellum and postscutellum simple. Mesopleura finely, closely punctate, and often with horizontal aciculation; anteriorly on prepectus with a sharp epicnemium; without a vertical carina or tubercle before middle coxae; episternauli, mesopleurauli, hypersternauli, and sternauli all absent, but episternal suture and mesopleural pit distinct; mesosternum rounded, not transversely carinate anteriorly. Propodeum variously aciculate; dorsal face without or with only a poorly defined trigonal area discally; posterior face with a shallow immarginate fovea discally; lateral carina wholly absent.

Fore legs with trochanters slender, obterete, elongate, generally more than one-half the length of fore femora; females and some males with a weak pecten on metatarsi. Middle tibiae with an apical calcar in both sexes. Hind tibiae strongly clavate; outer face more or less spinose; apically with two calcaria. Fore and middle metatarsi slender, straight; hind metatarsi somewhat thickened, slightly arcuate, and with a brush of short stiff setulae beneath. All metatarsi at least as long as the combined length of the four distal segments.

Fore wings with marginal cell at least twice as long as broad and broadly, squarely truncate at apex, furnished there with a large incomplete appendicular cell which is broadly open at apex; transverse cubital vein

straight, oblique, inclivous, joining the radial vein at about its middle; recurrent vein received on cubitus about its middle. Hind wing with anal lobe large, elongate, well separated off, and subequal in length to the submedian cell.

Abdomen sessile; fusiform; with or without maculation; impunctate or at most finely, sparsely acupunctate. Tergites folded under roundly and imbricate with the flatly convex sternites. Basal acarid chambers present on second to penult tergites. Males without a pygidial area on ultimate tergite, and the apical sternites relatively simple and un-modified. Females with pygidial area on last tergite complete or incomplete, and either flat and trigonal or strongly narrowed and excavate apically.

ETHOLOGY

The large majority of the Pemphilidine wasps prey upon rather soft bodied insects, chiefly Diptera. The species of *Tracheliodes*, however, attack and provision their nests with worker ants of the Dolichoderine genera *Liometopum* and *Tapinoma*. All *Tracheliodes* possess a large, much thickened head, with the face strikingly broad below. This peculiarity, as Bequaert has pointed out,[5] is evidently adapted to their ant-hunting habits, since it makes the jaws with which they seize the ants much more powerful than is customary among the Pemphilidines as a whole. The same peculiarity is likewise noticeable in the members of the myrmecotherous genus *Encopognathus*, as well as the corisphages of the genus *Anacrabro*, and the species of *Entomognathus* which attack Halticid beetles.

In 1933 during late July and early August, Hicks discovered *Tracheliodes hicksi* hovering above worker ants of the genus *Liometopum* which were marching in files up and down the trunks of small pine trees growing in Boulder Canyon, two miles west of the city of that name in Colorado. From time to time, the wasp would pounce down, grasp an ant and fly swiftly away, alighting on some nearby horizontal plane where the ant was stung before being conveyed to the nest. Despite much search of sumac and other plants with stems of a similar nature, as well as careful scrutiny of areas with varied types of soil and sand during the nesting season, Hicks was unable to locate the nest of this wasp. These brief but illuminating notes are the only recorded biological data on any Nearctic *Tracheliodes*.[6] However, as a result of the published observations of Emery,[7] Bignell,[8] Bequaert,[9] and particularly those of Ferton[10] and Grandi,[11] the

[5] Bull. Amer. Mus. Nat. Hist., XLV, p. 284, (1922).

[6] Hicks, C. H. Tracheliodes hicksi Sandhouse Hunting Ants. *Ent. News*, XLVII, pp. 4–7 (1936).

[7] Emery, C. Sur un Crabonide chasseur de Fourmis (Brachymerus curvitarsis H.-Sch.). *Bull. Soc. Ent. France*, 1893, pp. lxiii–lxiv (1893).

[8] Bignell, G. C. Crabro quinquesignatus Jurine, carrying ants off in Corsica. *Entom. Monthly Mag.*, XXXVI, p. 264 (1900).

life histories and habits of the two European species of this genus are known in considerable detail.

Both Ferton and Grandi have given rather full and excellent accounts of the life and activities of *Tracheliodes 5-notatus* (Jurine). This species nests in the ground, preferably in sandy soil, where it excavates cells, usually shallow in depth but sometimes quite long. At both Bonifacio in Corsica and at Algiers, Ferton states the burrows are seldom more than 4 cm. below the surface of the ground. Grandi's observations at Viserba and San Vincenzo in Italy on the whole confirm those of Ferton; but at the former locality he excavated a gallery which penetrated horizontally 20–30 cm. into a bank of hard sand. However, in view of the fact that no *Tracheliodes* is very well adapted for digging it may be that in this instance the wasp had merely utilized the abandoned burrow of another fossor; Ferton states that *Tracheliodes 5-notatus* is apt at times to resort to this practice. The nesting site chosen by *Tracheliodes 5-notatus* is quite diverse: talus slopes, sandy banks, sides of paths and roads, even old walls, all appear to be acceptable situations. The nest of *Tracheliodes curvitarsus*, however, is located in the abandoned holes constructed in trees by wood-boring beetles like Cerambycids. Hicks' inability to locate the burrow of the Nearctic form *T. hicksi* is probably due to the fact that it nests in situations similar to that chosen by the European *T. curvitarus*.

All the species of *Tracheliodes* capture their prey in essentially the same manner. The female wasp hovers above the foraging columns of *Liometopum* or *Tapinoma*, selects its victim, then suddenly pounces down, seizes an ant in its mandibles and immediately flies away with its prey.

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[9] Bequaert, J. C. The Predaceous Enemies of Ants: (Hymenoptera: 1.—*Tracheliodes 5-notatus* Jurine; 2.—*Tracheliodes curvitarsus* H.-Sch.). *Bull. Amer. Mus. Nat. Hist.*, XLV, pp. 283–284 (1922).

[10] Ferton, Ch. Un Hyménoptère ravisseur de Foumis. *Act. Soc. Linn. Bordeaux*, XLIV, pp. 341–346 (1892). [*Tracheliodes 5-notatus* (Jur.) under designation *Fertonius lutei-collis* Lepelletier.]

——— Nouveaux Hyménoptères fouisseurs et observations sur l'instinct de quelques espèces. *Act. Soc. Linn. Bordeaux*, XLVIII, pp. 260–272 (1986). [*Tracheliodes 5-notatus* (Jur.) under the designation *Fertonius formicarius* Ferton; pp. 268–270.]

——— Chap. II.—6: Chasseurs de Fourmis: Le Brachymère, pp. 146–151 [in his *La Vie des Abeilles et des Guêpes* edited by E. Rabaud & F. Picard, Paris, E. Chiron, 1923.] [*Tracheliodes 5-notatus* (Jur.) under the designation *Brachymerus luteicollis* (Lep.).]

[11] Grandi, G. Contributi alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori, VI: 16.—*Tracheliodes 5-notatus* Jurine. *Boll. Lab. Ent. R. Ist. Sup. Agr. Bologna*, I, pp. 19; 23–27 (1928).

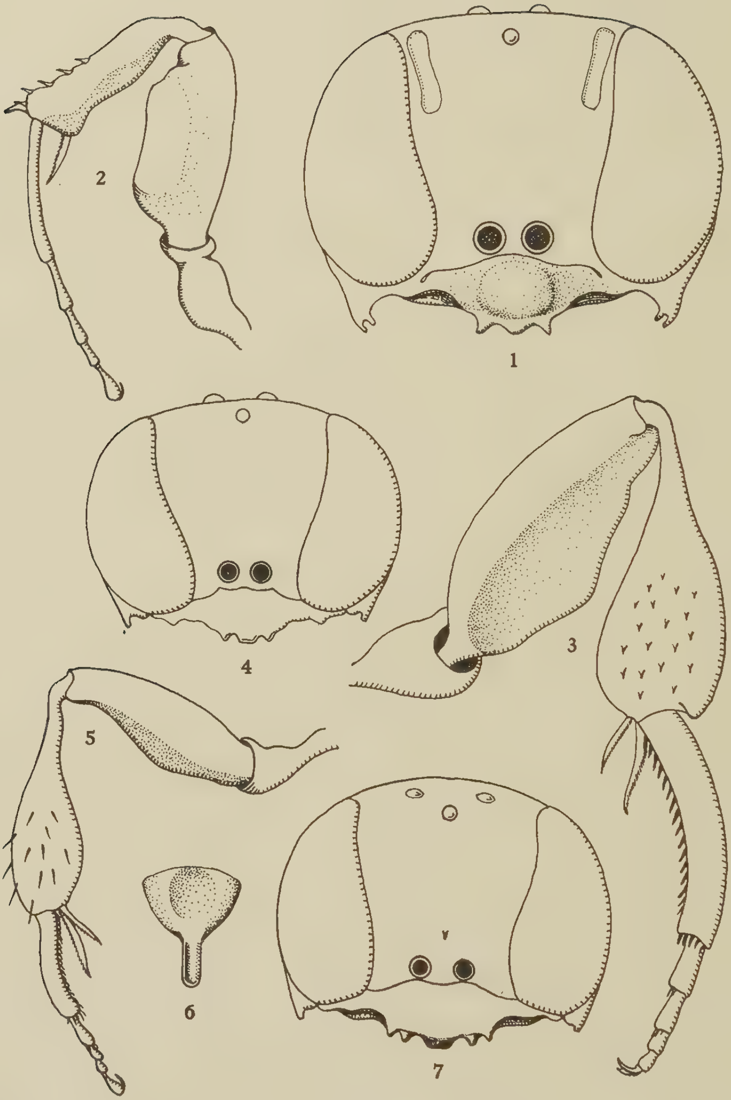
——— Specificità ed eterogeneità delle vittime degli Imenotteri predatori specializzione di comportamento delle femmine nidificanti e necessita dietetiche della loro larve. (10° Contributo alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori.) *Mem. R. Acad. Sci. Ist. Bologna, Class Sci.: Sez. Sci. Nat.* (8), VII, pp. 75–79 (1930).

——— Contributi alla conoscenza degli Imenotteri melliferi e predatori, XIII: 9.—*Crabro* (*Tracheliodes*) *5-notatus* Jur. *Boll. Lab. Ent. R. Ist. Sup. Agr. Bologna*, VII, pp. 32–35 (1934).

——— Contributi alla conoscenza degli Imenotteri Aculeati, XV: 9.—*Tracheliodes 5-notatus* Jur. *Boll. Lab. Ent. R. Ist. Sup. Agr. Bologna*, VIII, p. 45 (1935).

The ants, as the wasp hovers above their files preparatory to selecting a victim, apparently sense the peril that lurks above, for many of them rear up upon their hind legs, open their mandibles menacingly, and assume a generally threatening attitude. In the case of the Nearctic form *Liometopum apiculatum luctuosum*, Hicks noted that at times a given ant, apparently realizing its danger, substantially accelerated its pace up the trunk of the tree in a frantic endeavour to escape its probable and inexorable fate, or in a few instances plunged to safety on the ground, whereupon the wasp turned her attention toward another prospective victim. As soon as the ant has been captured, the wasp flies swiftly away to some convenient nearby point where it will be undisturbed and free from counter attacks by the victim's aroused comrades; this point may be either on the ground, as in the case of *T. 5-notatus*, or like *T. hicksi*, the limb of a tree or shrub: there the ant is stung, presumably in the thoracic or cervical region, and then conveyed to the nest. Each cell is provisioned with a rather tightly packed mass of ants, usually varying in number anywhere from 20 to 50 to a cell. But at San Vincenzo near Leghorn, Italy, Grandi found a completed cell with as few as nine ants and the egg of the wasp; while from one nest at Viserba on the Adriatic littoral he took as many as 94 *Tapinoma* workers.

Oviposition apparently does not occur until the cell has been fully provisioned. The egg, 2 mm. long, barely three-fourths of a millimeter in width, distinctly curved, and dirty white in color, is deposited on an ant about a third of the way from the bottom of the cell. It is firmly attached by its anterior end crosswise to the victim's mesosternum just behind the fore coxae; the posterior end of the egg juts out a considerable distance sidewise beyond the body of the ant. Ferton has advanced the theory that the wasp chooses this particular position in order that its delicate egg may be protected from shock occasioned by any sudden or violent movements of the prey. For Emery, Ferton, and Grandi all agree the ants are quite imperfectly paralyzed; for several days after being stung and stored they open and shut their mandibles incessantly, and move their antennae and legs continually. Indeed, Grandi records an ant that, when taken from the cell in which it had been stored, was able to scurry away, apparently in nowise injured by the trying ordeal to which it had been subjected. But in most cases the ants, though relatively active at first, are unable to support themselves or to walk if removed from the cell. Moreover, after a few days incarceration in the wasp's burrow, all visible traces of activity on their part disappear, and they gradually become more or less moribund. Although there may be some justification for Ferton's theory regarding the emplacement of the egg, it is much more likely, if a reason must be adduced for the wasp's action, that the particular place chosen is to enable the relatively weak and feeble newly hatched larva to find immediately a suitable



Tracheliodes foveolineatus (Viereck); female (type: Shasta Co., California): Fig. 1.—Anterior aspect of head. Fig. 2.—Middle leg. Fig. 3.—Hind leg. Fig. 6.—Pygidium.

Tracheliodes amu new species; male (type: Pecos, New Mexico): Fig. 4.—Anterior aspect of head. Fig. 5.—Hind leg.

Tracheliodes hicksi Sandhouse; male (allodigm; Post Creek Canyon, Pinaleno Mts., Arizona): Fig. 7.—Anterior aspect of head.

(All figures drawn to approximately same scale.)

place for attacking the soft tissues of the stored victim—in this case through the soft conjunctival membrane just behind the fore coxae.

The egg of the wasp hatches in about forty-eight hours, according to Ferton, and from it emerges a lively little whitish larva which straightway proceeds to feed upon the stored ants. Grandi has described and illustrated in considerable detail the immature stages of *Tracheliodes 5-notatus*. The larva is a bright yellowish-white, apodous, eyeless grub-like creature with an elongate, somewhat depressed body about 7 mm. in length; anteriorly it is quite slender, becoming progressively wider posteriorly until the maximum breadth of about 3 mm. is reached at the fifth and sixth abdominal segments; thence it tapers rapidly toward the posterior end. After consuming the soft internal tissues of the stored provender, the wasp grub pupates but first, however, it constructs a cocoon. This is a pale yellow, delicate, thimble-like structure, 7–8 mm. in length and 4–4.5 mm. in breadth: from the broadly rounded anterior end it is gradually ampliate posteriorly, terminating in a circular disc-shaped operculum whose diameter is slightly greater than that of the body of the cocoon. This operculum is firmly attached to the wall of the larval chamber; the remainder of the cocoon is free, projecting into the midst of the debris of ants which fill the cell. The walls of the cocoon are soft and flexible, composed of closely woven silken threads of various calibers cemented together into a homogeneous mass: fragments of ant-debris are usually affixed to the exterior and form a protective envelope for the cocoon.

In the summer, eclosion occurs in about three weeks. At Algiers, Ferton noted that *Tracheliodes 5-notatus* was multivoltine. Females of the first generation he observed had begun constructing their nests the first of July; these were completed and fully provisioned by the fifteenth of the same month and the adults emerged about the tenth of August. At the same place on the 25th of August, another batch of wasps, probably daughters of the first generation, were seen busily at work digging and provisioning their burrows which were finished the middle of September; the adults of this brood emerged October 6. At another site nearby on October 10, a third group of wasps was observed beginning nesting operations.

The data now available indicate that each species of *Tracheliodes* restricts its attacks to, and provisions its nests with, but a single species of ant: *Tracheliodes 5-notatus* to *Tapinoma erraticum*, *T. curvitarsus* to *Liometopum microcephalum*, and *T. hicksi* to *Liometopum apiculatum luctuosum*. It is my belief that every species of *Liometopum*, past and present, has had, or now has, a specific counterpart in the genus *Tracheliodes*. This thesis is elaborated in the ensuing discussion on the distribution of the genus and summarized in the following table.

Like many other fossorial Aculeates, the burrows of *Tracheliodes* are subject to the attacks of marauding Dipterous and Hymenopterous social parasites. At Viserba on Italy's Adriatic littoral, Grandi observed two

TABLE 1. *Probable interrelationship of species of Tracheliodes with dolichoderine ants.*

WASP—PREDATOR	ANT—PREY	RANGE
Tracheliodes 5-notatus	*Tapinoma erraticum*	Throughout Mediterranean Region
†*Tracheliodes* ?	*Liometopum lindgreeni*	Burma and Assam‡
Tracheliodes curvitarsus	*Liometopum microcephalum*	Germany to Sicily; southeastern Europe through Asia Minor to Caucasus.
†*Tracheliodes foveolineatus*	**Liometopum occidentale*	Oregon‡; California
Tracheliodes hicksi	*Liometopum apiculatum luctuosum*	Colorado; Arizona; New Mexico‡; California‡
†*Tracheliodes amu*	**Liometopum apiculatum apiculatum*	New Mexico; Colorado‡; to Old Mexico
†*Tracheliodes mortuellus*	**Liometopum miocenicum* (or *L. scudderi* ?)	Colorado: (Miocene) Florissant beds
? ?	*Liometopum antiquum*	Croatia: (Miocene) Radoboj beds
? ?	*Liometopum oligocenicum*	Baltic Amber (Oligocene)

*=probable prey (ant).
†=probable predator (wasp).
?=wasp (predator) unknown.
‡=no records of wasp from these areas although it probably occurs there.

unwelcome parasitic guests of *Tracheliodes 5-notatus:* and Anthomyid fly, *Hammomyia sociata* Meigen, and a Mutillid wasp, *Mutilla rufipes* F. Later at San Vincenzo near Leghorn, Grandi noted two other parasitic forms which he believed lived at the expense of the same species of wasp: the Miltogrammine fly, *Miltogramma punctatum* Meigen, and the Chrysid wasp, *Chrysis Leachii* Shuckard. These four social parasites have been recorded from the nest of many other fossorial bees and wasps in Europe. Close relatives of each of these cleptobionts occur in the Nearctic Region, and, when the ethology of the North American *Tracheliodes* is known in detail, will doubtless eventually be discovered in the nests of these wasps.

DISTRIBUTION

As here understood, *Tracheliodes* is a relict entity confined to the Holarctic Region, with the probable exception of an area in Burma and Assam as indicated below. Two Palaearctic forms, *5-notatus* and *curvitarsus*, are broadly distributed throughout central and southern Europe and the Mediterranean region; while the four Nearctic species: *amu*, *hicksi*, *foveolineatus*, and the Florissant Miocene fossil *mortuellus*, occur only in western North America.

In 1926 Arnold described two Ethiopian species: *perarmatus*[12] and *senex*,[13]

[12] *T[hyreopus]* (*Tracheliodes*) *perarmatus* Arnold, Ann. Transvaal Mus., XI, p. 349, figs. 5, 5a–c (1926); [♀; BÈLGIAN CONGO: Moho, near Lesse].

[13] *T[hyreopus]* (*Tracheliodes*) *senex* Arnold, Ann. Transvaal Mus., XI, p. 350, figs. 6, 6a

which he assigned to *Tracheliodes*. However, as indicated elsewhere in a review of the New World components of the Foxita complex,[14] I believe Arnold was misled in referring these African species to the present genus: the only characters they have in common with *Tracheliodes* are the three-segmented labial palpi and the rather elongate fore trochanters; the remaining features insofar as I can determine from the descriptions and figures of Arnold, are markedly similar to those displayed by the members of the Foxita complex, and I have therefore tentatively relegated them to that group.[14] Furthermore, aside from the structural differences of these African wasps, no ants of the genus *Liometopum*, with which, as demonstrated below, the species of *Tracheliodes* are almost invariably associated, are known from the Ethiopian Region. But although considerable weight may be attached to this last fact, nevertheless it may not be regarded as conclusive evidence that *Tracheliodes* is absent from the Ethiopian Region. For *5-notatus*, one of the two Palaearctic species of *Tracheliodes*, preys upon ants of the closely related Dolichoderine genus *Tapinoma* of which ten species have been recorded from Africa south of the Sahara.[15] However, notwithstanding this, I believe it quite improbable that *Tracheliodes* as here understood will ever be found in the Ethiopian fauna.

With the exception of the European *5-notatus*, the distribution of *Tracheliodes* and its component species is curiously correlated with, and apparently limited by, those of the ant *Liometopum* upon which these wasps prey. A brief resume of this Dolichoderine genus may thus contribute materially to an understanding of the distribution of *Tracheliodes*. Five modern forms of *Liometopum* are known: *L. microcephalum* occurs in southern Europe and Asia Minor, *L. lindgreeni* in Burma and Assam,—and in western North America, *L. apiculatum apiculatum*, *L. apiculatum luctuosum*, and *L. occidentale*. In addition to the foregoing recent forms, four fossil species[16] have been described: the Baltic Amber contains one species, *L. oligocenicum;* the Croatian Radoboj beds another, *L. antiquum;* and the Miocene shales at Florissant in Colorado two: *L. miocenicum* and *L. scudderi;* the first is Lower Oligocene in age, the remainder later, Miocene species.

Two of the extant *Liometopa* are definitely associated with species of

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(1926); [♂; Southern Rhodesia: Helenvale].—Arnold, Ann. Transvaal Mus., XX, p. 137 (1940); [Southern Rhodesia: ♀, Lupane; ♂, Khamis].

[14] *Cf.* Pate: The New World Genera and Species of the Foxita Complex. *Revista de Entomologia* (Rio de Janerio), XIII, (1942).

[15] *Cf.* Wheeler: Bull. Amer. Mus. Nat. Hist., XLV, pp. 923–925; 1034 (1922).

[16] According to Carpenter (1930, Bull. Mus. Comp. Zoöl., LXX, pp. 17–18), the Eocene fossil ant *Liometopum pingue* which Scudder described from the Green River beds in Wyoming and the White River beds in Utah, is a member of the genus *Eoformica*. I know nothing about *L. imhoffi* and *L. schmidti* which Heer described from the Lower Miocene beds at Radoboj in Croatia; they may be synonyms of *L. antiquum* Mayr, or perhaps now referred to another genus.

Tracheliodes: the Nearctic *L. apiculatum luctuosum* with *T. hicksi;*[17] and the European *L. microcephalum* with the wasp *T. curvitarsus* whose range, Kohl states,[18] is limited by the distribution of the ant. The Californian form, *Tracheliodes foveolineatus*, whose nearest relative is *T. curvitarsus* of Europe, inhabits the same general area as the Nearctic ant *Liometopum occidentale*, the North American counterpart of the Palaearctic *L. microcephalum;* in view of this close double kinship, it is only logical to assume *Tracheliodes foveolineatus* attacks the ant *L. occidentale* whose range[19] accordingly no doubt in great measure conditions the distribution of that wasp. The Burman *L. lindgreeni* and the nominate race of the Nearctic *L. apiculatum* are not as yet definitely associated with a *Tracheliodes.* But since the wasp *amu* occurs in the same region and faunal zone as the latter ant, it is not unreasonable to infer the two are correlated, and that the range of the ant *L. apiculatum apiculatum*[20] probably determines to a large extent that of the wasp *amu.* The Burman ant *L. lindgreeni* is at present without any known counterpart in *Tracheliodes;* but in view of the foregoing evidence, it may be predicted that such a species of wasp certainly exists and will eventually be discovered.[21] According to Carpenter,[22] two of the commonest ants in the Miocene shales at Florissant, Colorado, are *Liometopum miocenicum* and *L. scudderi;* it is not illogical to suppose that one of these, *miocenicum* perhaps, formed the prey of the primordial wasp *Tracheliodes mortuellus* which Cockerell described from the same beds. And finally, it is likewise very probable that species of *Tracheliodes* co-existed with, and victimized, the Baltic Amber *Liometopum oligocenicum,*[23] as well as the Miocene form *L. antiquum* of the Radoboj shales, but whether these wasps will ever be found is, of course, a matter of pure chance.

The foregoing exposition clearly demonstrates the intimate relationship existing between *Tracheliodes* and *Liometopum.* Consequently the phylogenetic history of the wasp in all probability closely parallels that of the ant. And for the latter, Wheeler, following the thesis of mammalian dispersal brilliantly elaborated by the late William Diller Matthew,[24]

[17] *Cf.* Hicks: Ent. News, XLVII, p. 5 (1936); *V. et.:* discussion of the distribution of *T. hicksi* on a following page.

[18] *Cf.* Kohl: Ann. K. K. Naturhist. Hofmus. Wien, XXIX, p. 328. (1915).

[19] *Cf.* Wheeler: Proc. Amer. Acad. Arts & Sci., LII, p. 522 (1917).

[20] *Cf.* Wheeler: Proc. Amer. Acad. Arts & Sci., LII, p. 521 (1917).

[21] Seventy or more Oriental Pemphilids are now known, and of this number at least ten are recorded from Burma and Assam. It may thus be that Cameron, Bingham or Turner have already unwittingly characterized this missing modern *Tracheliodes;* in the main, their descriptions are unfortunately too inadequate to enable one to allocate the species to their proper genera and subgenera without a re-examination of the types.

[22] *Cf.* Carpenter: Bull. Mus. Comp. Zoöl., LXX, p. 24, (1930).

[23] Brischke in his summary of the genera of Hymenoptera known from the Baltic Amber (Lower Oligocene) mentions (Schrift. Naturf. Gesellsch. Danzig (N. F.), 6, iii, pp. 278–279, 1886) a *Crossocerus:* this might, upon examination, prove to be a *Tracheliodes.*

[24] W. D. Matthew: Climate and Evolution. Ann. N. Y. Acad. Sci., XXIV, pp. 171–318

postulates a Palaearctic origin in the neighbourhood of Transcaspia or central Asia.[25] Furthermore, he opines that since the early Tertiary fossils of these ants are quite as highly specialized as their existing congeners, the genus *Liometopum* goes back at least to the Palaeocene or perhaps even to the Upper Cretaceous.[26] A similar origin and co-evality may accordingly be attributed to *Tracheliodes*, although naturally the age of the wasp is without question more recent than that of the ant.

From their original home in central Asia, the primeval *Liometopa* spread westward, leaving behind their imprints in the Lower Oligocene Baltic Amber and the Miocene shales of Radoboj in Europe where but one species, *microcephalum*, has survived to the present day. Their dispersal eastward eventually resulted in an invasion of North America early in the Tertiary by way of the land connection then existing between Siberia and Alaska. And in this exodus from the Old World, the *Liometopa* were without doubt closely followed, if not accompanied by, their harrier counterparts in *Tracheliodes*. In time these primordial Nearctic immigrants became extinct, but some like *Liometopum miocenicum* and *scudderi* and *Tracheliodes mortuellus*, preserved for posterity in the Miocene shales at Florissant, Colorado, were undoubtedly closely related to, if not the direct ancestors of, the modern ants *apiculatum* and *luctuosum*, as well as the wasps *amu* and *hicksi*, living today in Colorado and New Mexico. To the descendants of this Miocene fauna were added later, probably during the Pliocene or early Pleistocene, the forebears of the present *Liometopum occidentale* and *Tracheliodes foveolineatus* by immigration from Eurasia over the Siberian-Alaskan land bridge. Subsequent glaciation and orogenic movements have extirpated much of the once vigorous and widespread *Liometopum* and *Tracheliodes* stock in the central areas until today only scattered remnants of these one time numerous and vagile populations are left, isolated in the peripheral areas of Europe, Burma, Assam, and western North America. In the Palaearctic Region one wasp, *T. 5-notatus*, evidently retained sufficient initiative to transfer its depredations to the closely related Dolichoderine ant *Tapinoma* as the decadent *Liometopum* stock waned to but one modern representative, but in North America, the long consociation of *Tracheliodes* with *Liometopum* has apparently become so fixed that the wasps have seemingly been incapable of adapting themselves to such eurythermal Nearctic ubiquists as *Tapinoma sessile*. For had they been able, then *Tracheliodes* would indubitably be found today in the eastern states, rather than restricted as at present to the cooler, more xeric montane areas of the west, there dependant largely on the presence of *Liometopum*. Like the ant, the extant species of *Tracheliodes* are obviously

(1915). *V. et.:* Spec. Publ. N. Y. Acad. Sci., No. 1, pp. 1–148 (1939).

[25] *Cf.* Wheeler: Proc. Amer. Acad. Arts & Sci., LII, p. 498 (1917).

[26] *Cf.* Wheeler: Proc. Amer. Acad. Arts & Sci., LII, p. 488 (1917).

but a small remnant of a large series of forms which probably comprised the genus in the mid-Tertiary.

Wheeler has commented upon the fact that the Nearctic forms *Liometopum occidentale* and *L. apiculatum luctuosum* are associated with live-oaks and the nominate race of *L. apiculatum* only with pines.[27] It might prove interesting therefore to ascertain whether each of these ants is definitely limited to one or more species of live-oaks and conifers. And if so, then the distribution of these plants might perhaps serve as a further index for the probable ranges of the Nearctic species of *Tracheliodes*.

Kohl has given such an excellent account of the Palaearctic species[28] that only the North American forms are treated in the following discussion.

KEY TO THE NEARCTIC SPECIES OF TRACHELIODES

1. Fossil forms; (Miocene beds, Florissant, Colorado) .... *mortuellus* Cockerell
   Extant forms 2
2. Scutellum, fore and middle legs, and abdomen, all largely bright yellow; front simple, unarmed; clypeus strongly tumid discally and tridentate medio-apically; (west coast forms ranging from western Oregon to southern California) .... *foveolineatus* (Viereck)
   Scutellum and abdomen immaculate black; clypeus flat discally 3
3. Clypeus, mandibles, scapes, pronotal tubercles, all trochanters, and fore and middle tibiae and tarsi, all light yellow; front simple unarmed; clypeus tridentate medio-apically; postocellar line one-half the length of the ocellocular distance; mesopleura with the episternal suture finely foveolate; (montane forms ranging from Colorado to central Mexico) .... *amu* new species
   Immaculate black except for ivory white stripes on outer faces of tibiae; front armed medially with a small porrect spinoid tubercle just above antennal sockets; clypeus quinquedentate medioapically; postocellar line at least four-fifths the ocellocular distance; mesopleura with the episternal suture simple, efoveate; (montane forms of the Rockies and Colorado Plateau of (Utah?), Colorado, New Mexico and Arizona, ranging westward into the Sierra Nevada and Transverse Ranges district of southern California) .... *hicksi* Sandhouse

TRACHELIODES MORTUELLUS Cockerell

Tracheliodes mortuellus Cockerell, Bull. Mus. Comp. Zoöl., Harvard Coll., L, p. 45 (1905).

Type.—Florissant, Colorado, Miocene (Tertiary) Shales. [Museum of Comparative Zoölogy, Type no. 2015 (S. H. Scudder Collection, no. 3200).]

At the present time I am unable to add anything to Cockerell's brief description of this species. The venation of the wings indicates it is evidently a Pemphilid, but the head is not preserved in such a position that certain important diagnostic features, *e.g.* the palpi, may be observed. Consequently I have assumed that Cockerell was correct in assigning *mortuellus* to *Tracheliodes*.

As indicated on a previous page, it is not unlikely that *mortuellus* preyed upon *Liometopum miocenicum*, a fossil Dolichoderine ant recorded in great numbers from the same beds at Florissant whence Cockerell described *Tracheliodes mortuellus*.

[27] *Cf.* Wheeler: Proc. Amer. Acad. Arts & Sci., LII, p. 521 (1917).
[28] Kohl: Ann. K. K. Naturhist. Hofmus, Wien, XXIX, pp. 322–328 (1915).

Tracheliodes amu,[29] new species

FIGS. 4 and 5.

The tridentate clypeus, simple unarmed front, high equilateral ocellar triangle, and the yellow mandibles, clypeus, antennal scapes, pronotum and legs immediately distinguish *amu* from *hicksi*. In these respects, the present species agrees somewhat with the west coast form *foveolineatus*, from which, however, *amu* is differentiated by its immaculate black abdomen, flat clypeus, non-striate mesonotum and pleura, and the appreciably shorter antennal scapes and antennocular distance.

Type.—♂; Pecos, San Miguel County, New Mexico. Elevation, about 7100 feet. June 23. (T. D. A. Cockerell.)

Male. 7 mm. long. Black; the following stramineous: mandibles except red apices, clypeus, scape, dorsal surface of pronotum with a transverse stripe medially, pronotal tubercles, all trochanters, fore and middle femora beneath, fore and middle tibiae and tarsi entirely, and hind tibiae on basal half of outer face. Light brunneous: pedicel, fore and middle femora above, hind tibiae except basal maculation, hind tarsi, and tegulae and axillary sclerites. Abdomen with posterior margins of first three tergites, and also the venter largely, testaceous. Wings clear hyaline, iridescent; veins and stigma brunneous.

Head subfulgid; clypeus and anterior aspect of front heavily clothed with appressed silvery sericeous pile; vertex and upper portion of front and temples with a thin, inconspicuous vestiture of puberulent hair, the lower temples with a denser, heavier clothing of longer, suberect silvery pubescence. Front and vertex with a microscopically fine cancellate sculpture upon which is superposed a series of scattered, widely separated, fine setigerous punctures; front relatively flat between the inner orbits which are subparallel to slightly convergent below, bisected above by a shallow, indistinct furrow running forward from the anterior ocellus, and simple, not armed with median spine or tubercle just above antennal sockets; supra-orbital foveae not evident; ocelli arranged in a high equilateral triangle, the postocellar distance one-half the length of ocellocular line; temples with fine setigerous acupunctures throughout. Antennae reaching about to occiput; scapes straight, cylindrical to somewhat obterete, four-tenths the vertical eye length; pedicel obterete, about seven-tenths (.715) the length of first flagellar article; flagellum simple, finely puberulent, first segment seven-sixths the length of the second, ultimate article simple, terete, one and two-fifths the length of penult segment; antennal sockets subcontiguous to each other but relatively remote from nearest lower inner orbit, the antennocular distance two and one-half times the length of the

[29] After the Amu or Ant Clan of the Pecos Indians of New Mexico; in allusion to the probable myrmecotherous habits of this wasp.

interantennal line. Clypeus transversely narrow-lenticular, flat laterally and discally, median length one-fourth the vertical eye length; medio-apically with a small, broad, truncate tooth, laterad of which on each side is a small rounded tooth. Mandibles stout; apices bidentate; lower margins simple, entire.

Thorax subfulgid; thinly clothed dorsally with an inconspicuous, suberect, puberulent pile, the pleura and sterna with more noticeable, longer, decumbent silvery hair. Pronotum transverse, short, finely punctate, rounded and ecarinate dorsally, the lateral angles bluntly rounded, very inconspicuously notched mediodorsally, the posterior margin strongly impressed. Mesonotum with microscopically fine cancellate sculpture upon which is superposed a series of very fine, rather close, setigerous acupunctures, anterior half with four parallel longitudinal impressions medially; sutures between mesonotum and scutellum, and scutellum and postscutellum deeply impressed and foveate; axillae small, immarginate laterally; scutellum and postscutellum simple, with sculpture and puncturation like mesonotum. Mesopleura with a sharp epicnemium anteriorly, episternal suture slightly arcuate and finely foveate; prepectus finely, closely punctate, the upper half of prepectus and mesopleura with fine, parallel, horizontal aciculation, remainder of surface with microscopically fine cancellate sculpture upon which is superposed a few widely scattered setigerous punctures; metapleura fulgid, hind margin finely consute, traversed by fine parallel horizontal aciculations which are continuous onto lateral faces of propodeum; mesosternum rounded, not transversely margined anteriorly. Propodeum fulgid; posterior and lateral faces with a thin vestiture of suberect light hair; dorsal face glabrous, with a large trigonal area not delimited posteriorly by a furrow or carinule, but traversed by fine striae radiating from anterior margin which is furnished with a transverse row of small foveae; posterior face traversed by parallel, horizontal aciculations continuous from the lateral faces, discally with a shallow immarginate lyrate depression; posterior lateral margins rounded; lateral carinae absent.

Legs relatively simple. Fore legs with trochanters slender, subobconical six-tenths the length of fore femora; metatarsi simple, not flattened nor provided with a pecten, and subequal in length to the four distal articles combined. Middle legs with the trochanters simple, obterete, one-half the length of femora; metatarsi slender, straight, weakly spined below, subequal in length to four distal segments combined, and about five-ninths (.566) the length of the simple, subfusiform tibiae whose apical calcar is not evident. Hind legs with tibiae strongly clavate apically, the outer face with a number of short, rather stout spines, and with two stout, elongate calcaria, the longer seven-tenths the length of metatarsi which are thickened, slightly arcuate, the lower concave surface with a dense brush of

short, erect, stiff hairs and a row of short declinate spines, five-ninths the length of tibiae and six-fifths the length of the four distal segments combined.

Fore wing with the marginal cell three times as long as wide and broadly squarely truncate at apex; radial vein with first abscissa four-fifths the length of second abscissa; transverse cubital vein oblique, inclivous, weakly sinuous, and five-ninths the length of second abscissa of cubitus which in turn is nine-tenths the length of first abscissa of cubitus.

Abdomen fulgid; rather slender and elongate. Tergites with fine transverse aciculation upon which is superposed a series of sparse and scattered acupunctures each bearing a short decumbent silvery hair. Second to penult tergites with basal acarid chambers; ultimate tergite subsemigaleate, without a pygidial area delimited. Sternites subnitidous, subglabrous.

Female. Unknown.

Distribution.—At present *Tracheliodes amu* is known only from high in the hills about Pecos, New Mexico. But this locality is well within the boundaries of the area Wheeler gives for the distribution of the Dolichoderine ant *Liometopum apiculatum apiculatum.*[30] And since the two North American congeners of *amu* are each apparently associated with, and thus without doubt areally limited by, the distribution of another Nearctic form of *Liometopum*, it seems not unreasonable to infer therefore that *amu* preys upon the nominate race of *L. apiculatum* and that the range of the latter to a large extent determines the distribution of this wasp. If this be so, then *Tracheliodes amu* is, like the typical race of *apiculatum*, a montane form of the Upper Sonoran and Transition Zones, ranging from the Rockies of north-central Colorado southward through the mountain areas of New Mexico and eastern Arizona well into Old Mexico.

TRACHELIODES HICKSI Sandhouse

FIG. 7.

Tracheliodes hicksi Sandhouse, Ent. News, XLVII, p. 2 (1936); [♀ Boulder County, Colorado]. Hicks, Ent. News, XLVII, pp. 4–7 (1936); [♀; Boulder County, Colorado; biological notes].

Type.—♀; Boulder Canyon, two miles west of Boulder, Colorado. Elevation, about 5500 feet. July 28, 1933. (Charles H. Hicks.) [United States National Museum, Catalogue no. 50488.]

The somber black habitus relieved only by narrow ivory white stripes on the outer faces of the tibiae easily differentiates *hicksi* from both its North American and European congeners. In addition, the clypeus of *hicksi* is quinquedentate apically and the front armed with a small median

[30] *Cf.* Wheeler: 1917, Proc. Amer. Acad. Arts and Sci., LII, p. 521. According to Wheeler, *Liometopum a. apiculatum* seems always to be associated with live-oaks. *V. et.:* Bull. Amer. Mus. Nat. Hist., XXI, pp. 321–333 (1905).

spine just above the antennal sockets, whereas in *foveolineatus* and *amu* the clypeus is tridentate while the front is simple.

Hitherto only the female of *hicksi* has been known. I now have before me a specimen which indubitably represents the opposite sex and of which a description is herewith appended.

Allodigm.—♂; Post Creek Canyon in the Pinaleño Mountains, near Fort Grant, Graham County, Arizona. July 18, 1917. [Cornell University.]

Male. 7 mm. long. Entirely black except for eburneous maculation on whole outer faces of fore and middle tibiae and basal two-thirds of hind tibiae. Wings clear hyaline, iridescent; veins and stigma brunneous.

Head subfulgid; subquadrate in dorsal and anterior aspects; clypeus and anterior aspect of front with a moderate vestiture of appressed silvery pubescence; vertex, temples, and dorsal aspect of front with scattered, erect, rather long hairs; temples thinly clad with appressed silvery puberulent pubescence. Front and vertex with a microscopically fine cancellate sculpture upon which is superposed a series of scattered, widely separated, setigerous punctures. Front broad, subquadrate, relatively flat, bisected by a fine line running forward from anterior ocellus, and medially just above antennal sockets with a small porrect spinoid tubercle; inner orbits subparallel to slightly convergent below; supra-orbital foveae not evident; ocelli arranged in a low triangle, the postocellar line nine-tenths the ocellocular distance; occipital carina distinct but neither flanged, foveolate, nor a complete circle in extent; temples with fine acupuncturation throughout. Antennae reaching about to occiput, situated low on face on dorsal margin of clypeus, the sockets subcontiguous to each other but remote from nearest lower inner orbit, the antennocular distance two and a third times the length of the interantennal line; scapes cylindrical, straight to very slightly bowed, three-sevenths (.43) the vertical eye length; pedicel obeterete, five-sevenths (.715) the length of first flagellar article; flagellum simple, finely puberulent, second segment about seven-tenths (.715) the length of first, ultimate article simple, terete, one and two-fifths the length of penult segment. Clypeus transverse lenticular, median length about one-fourth (.263) the vertical eye length, flat laterally and discally, produced medio-apically into a short broad subtruncate lobe whose apical width is one and a half the median clypeal length, and whose apical margin is welted and roundly emarginate laterally on each side resulting in a broad subtruncate tooth medially and a sharp one at each distolateral angle; laterally on each side of lobe and separated from it by a deep rounded emargination with another strong tooth, the clypeus thus quinquedentate. Mandibles stout; apices bifid; lower margins simple entire.

Thorax subfulgid; dorsum and pleura with a thin and scattered vestiture of rather long, erect light hair; sternum more heavily clothed with appressed silvery pubescence. Pronotum short, transverse, finely punctate,

dorsal surface rounded, ecarinate, lightly notched medially, posterior margin deeply impressed, lateral angles bluntly angular. Mesonotum with microscopically fine cancellate sculpture upon which is superposed a series of very widely separated setigerous acupunctures, anterior third bisected by a fine double line; axillae small, immarginate; scutellum with sculpture and puncturation like mesonotum, anterior margin consute, lateral edges immarginate; postscutellum simple, finely punctate, anterior margin finely consute. Mesopleura with sculpture and puncturation like mesonotum, anteriorly with a sharp epicnemium, episternal suture sinuous, simple and efoveate, mesopleural pit inconspicuous, upper half behind episternal suture with fine parallel horizontal costulae, posterior margin simple, efoveate; metapleura sculptured like upper half of mesopleura; mesosternum rounded, immarginate anteriorly. Propodeum with posterior and lateral faces with a thin clothing of conspicuous long, suberect, light hair; dorsal face without a delimited trigonal area discally, but finely and radiately aciculate from anterior margin which has a transverse row of small foveae; posterior face laterally with horizontal aciculation which curves up vertically mesad, discally with a shallow, immarginate, cuneate depression; posterior lateral corners broadly rounded; lateral carinae absent; lateral faces horizontally aciculate.

Legs relatively simple. Fore legs with trochanters slender, subobconical, slightly more than half (.53) the length of simple femora; metatarsi simple, straight, with a row of short stiff spines below, five-fourths the length of four distal segments combined and two-thirds the length of simple tibiae. Middle tibiae with trochanters simple, obterete, one-half the length of simple subfusiform femora; metatarsi slender, straight, twice the length of four distal segments combined, and two-thirds the length of slender, obterete tibiae which are armed with a distinct apical calcar. Hind legs with femora subfusiform and shallowly concave lengthwise below on lower anterior face; tibiae slender basally to strongly clavate apically, outer face moderately spinose; five-thirds the length of metatarsi, and apically with two calcaria, the longer one-half the length of metatarsi which are thickened, slightly arcuate, with a brush of short erect stiff hairs on lower concave surface, and six-fifths the length of four distal segments combined.

Fore wing with marginal cell three times as long as wide, broadly and squarely truncate at apex; radial vein with first abscissa four-fifths the length of second abscissa; transverse cubital vein straight, oblique, inclivous, five-ninths the length of second abscissa of cubitus which is subequal to first abscissa of cubitus.

Abdomen slender, elongate; more or less fulgid; thinly clothed with a sparse vestiture of decumbent puberulent hair, and finely, sparsely acupunctate. Second to penult tergites with distinct basal acarid chambers; ultimate tergite subsemigaleiform, and without a pygidial area. Sixth

sternite with a deep trigonal cleft medio-apically; seventh sternite flat, entire.

The female sex, described by Miss Sandhouse from a unique specimen taken near Boulder, Colorado, apparently conforms in all essential particulars with the foregoing characterization of the male, except in the following details:

On the head, the supra-orbital foveae are large, distinct, and elongate-linear in shape; the postocellar distance is only four-fifths the length of the ocellocular line; and the first flagellar article is four-thirds the length of the second segment. The anterior trochanters are five-eighths the length of the fore femora; while the sixth abdominal tergite is provided with a distinct pygidial area which is strongly narrowed apically, grooved medially, and with the side of the apical portion nearly parallel and ecarinate.

Distribution.—The only localities known at present where *hicksi* has been taken are in the Pinaleño Mountains of Arizona and Boulder Canyon, two miles west of the city of that name, in central Colorado. At the latter spot, Hicks,[31] for whome the present species was named, observed this wasp following and capturing ants of an undetermined species of *Liometopum*[32] marching in columns along the trunks of small pine trees. These ants, I presume, were *luctuosum*, the atypical race of *Liometopum apiculatum*, since, according to Wheeler, this is the only Nearctic form of that Dolichoderine genus associated with conifers.[33] Both places where the wasp has been caught are within the area Wheeler gives for *luctuosum*, and the distribution of *hicksi* accordingly probably coincides more or less with the range of that ant.[34] Assuming therefore this inference is correct, *Tracheliodes hicksi* is a montane species of the Upper Sonoran and Transition zones of western and southwestern United States; its range presumably extends from the Rockies of north-central Colorado, and perhaps Utah, south and westward through the mountain regions of the Colorado Plateaux into the Transverse Ranges district[35] of southern California, and thence northward along the Sierra Nevada at least as far as the Yosemite in central California.

[31] Ent. News, XLVII, pp. 4–7 (1936).

[32] Genus determined by T. D. A. Cockerell, according to Hicks.

[33] Wheeler states (1917, Proc. Amer. Acad. Arts & Sci., LII, p. 521): " . . . Though rarer and more sporadic than the typical form of the species [i. e. *Liometopum apiculatum apiculatum*] and *occidentale*, this subspecies [*i.e. L. apiculatum luctuosum*] seems to have a wide range. The few colonies seen in the Yosemite were running on pine trees. This seems to confirm the opinion I advanced in 1905 [Bull. Amer. Mus. Nat. Hist., XXI, pp. 321–333] that *luctuosum* is definitely associated with conifers."

[34] *Cf.* Wheeler: Proc. Amer. Acad. Arts & Sci., LII, p. 521 (1917). *V. et.:* Rees and Grundmann (1940, Bull. Univ. Utah, XXXI, no. 5, p. 6) who record *Liometopum apiculatum luctuosum* from the following localities in Utah: Gunnison Butte, on Gree River; Myton, Duchesne Co. Moab, Grand Co.; and Hatch Wash near La Sal, San Juan Co.

[35] San Gabriel and San Bernardino Mountains.

TRACHELIODES FOVEOLINEATUS (Viereck)

FIGS. 1, 2, 3, 6.

Crabro (*Cuphopterus*) *foveolineatus* Viereck, Proc. Ent. Soc. Washington, XI, p. 44, fig. 2 b (1909); [♀ ; Shasta Co., California].

The bright yellow mandibles, clypeus, antennal scapes, pronotum, scutellum, legs, and abdominal fasciae, and in addition the simple unarmed front, tumid clypeus, and the peculiar and characteristic conformation of the middle and hind legs readily distinguish *foveolineatus* from its Nearctic congeners *hicksi* and *amu*.

Type.— ♀ ; Shasta County, California. (No other data.) [Academy of Natural Sciences of Philadelphia, Type no. 4994.]

Female. 8 mm. long. Black; the following citrinous: mandibles save red apices, clypeal disc, scapes, temples just above bases of mandibles, pronotum dorsally to and including the tubercles and prepectus with a large spot just behind latter, scutellum entirely, tegulae with a small discal spot, outer margins of axillary sclerites, fore and middle legs distad of coxae, hind coxae, hind tibiae with basal half annulate and all of outer faces except extreme apex, and on abdomen: first tergite with apical half and all of inflexed ventral portion, second to fifth tergites entirely save for a narrow transverse black band at base and a testaceous caudal border, the fifth bisected by a dark longitudinal line; second sternite entirely except for a pair of fulvous discal spots, a median emargination posteriorly and a narrow transverse band along posterior margin, third and fourth sternites save for posterior margin and a median caudal emargination. Dark fulvous: palpi, hind metatarsi, fifth sternite and all of ultimate abdominal segment, tegulae and axillary sclerites. Wings clear hyaline, iridescent; veins and stigma light brunneous.

Head subfulgid; subquadrate in anterior and dorsal aspects; clypeus with a thin vestiture of short, decumbent, light aeneous setulae; front, particuarly along inner orbits, with a thin pile of appressed silvery pubescence; vertex and temples with an inconspicuous vestiture of short, decumbent subaeneous hair. Front finely, closely punctate, simple and unarmed with a spine or tubercle medially just above antennal sockets, and broadly, shallowly concave between the inner orbits which are subparallel to slightly convergent below. Vertex with microscopically fine cancellate sculpture upon which is superposed a series of irregularly scattered, moderately fine punctures; supra-orbital foveae large and distinct, opaque, contiguous to and paralleling upper third of inner orbits, their posterior ends opposite anterior margin of hind ocelli, elongate-linear in shape, their width three-fifths the diameter of an ocellus, their length eight times their breadth; ocelli situated in an equilateral triangle, the postocellar line almost six-tenths (.586) the ocellocular distance; temples moderate, and finely, rather closely punctate; occipital carina distinct but

neither flanged, foveolate, nor a complete circle in extent. Antennae situated low on face on dorsal margin of clypeus, the sockets remote from lower inner orbits but subcontiguous to each other, the interantennal line two-sevenths (.285) the antennocular distance; scapes simple, obterete, escarinate, one-half the vertical eye length; pedicel obterete, six-tenths the length of first flagellar article; flagellum simple, finely puberulent, first segment one and three-tenths the length of second, ultimate article simple, terete, one and two-fifths the length of preceding segment. Clypeus transverse, median length one-fourth the vertical eye length; short, linear and strongly concave laterally to strongly tumid discally; produced medially into a short broad truncate lobe, the apical margin of which has a broad rounded tooth medially and a sharp tooth at each distolateral angle. Mandibles stout; apices bidentate, the lower tooth shorter; lower margin simple, entire.

Thorax more or less fulgid; with a thin, inconspicuous, light aeneous pubescence dorsally and on pleura which in addition have a few decumbent aeneous setulae below and on sterna. Pronotum short, transverse, gibbous, finely punctate, ecarinate dorsally but inconspicuously notched medially there, the lateral angles rounded, the posterior margin very strongly impressed. Mesonotum very finely longitudinally aciculate and with a superposed series of scattered, widely separated, moderate setigerous punctures, the anterior half bisected by three parallel longitudinal lines; suture between mesonotum and scutellum impressed; axillae small, simple, immarginate laterally; scutellum flat, with inconspicuous longitudinal aciculation and scattered fine punctures, anterior margin foveate, lateral edges simple, immarginate; postscutellum simple, flat, finely punctate. Mesopleura strongly, horizontally aciculate; prepectus anteriorly with a sharp epicnemium; episternal suture strongly foveolate; mesopleural pit evident; hind margin finely consute. Metapleura horizontally aciculate. Mesosternum rounded, not transversely carinate anteriorly. Propodeum fulgid and glabrous save for a very thin vestiture of short, suberect, light hair on posterior face; dorsal face very finely and longitudinally to radiately aciculate, without a distinct trigonal enclosure but with a row of small foveae along anterior margin; lateral faces with horizontal aciculation continuous onto posterior face which has an immarginate, obpyriform, opaque fovea discally; lateral carinae absent.

Fore legs with trochanters slender, obconical, elongate, five-elevenths the length of stocky subtriquetrous femora; tibiae relatively simple but strongly flattened beneath; tarsi simple, not appreciably flattened, metatarsi straight, with a pecten of short stout bristles, and five-elevenths the length of tibiae and subequal in length to four distal segments combined. Middle legs with trochanters thick, broadly and shallowly concave beneath on distal half, and four-sixths the length of femora which are weakly

and concavely flattened on posterior face, their lower edge weakly subtrenchant lengthwise; tibiae with one apical calcar; metatarsi slender, inconspicuously arcuate, spined below, three-fourths the length of tibiae, and subequal in length to four distal segments combined. Hind legs with femora subfusiform, their lower anterior faces abruptly concave lengthwise below, the lower margin with a subtrenchant edge which is obtusely angulate medially; tibiae slender basally to strongly clavate apically, the outer face furnished with short, stiff spines, apically with two slender acuminate calcaria, the longer one-half the length of metatarsi which are thickened, arcuate, with a brush of short stout setulae beneath, five-eighths the length of tibiae and five-fourths the length of four distal segments combined.

Fore wings with marginal cell three times as long as wide, and broadly, squarely truncate at apex; radial vein with first abscissa five-sixths the length of second; transverse cubital vein oblique, inclivous, somewhat sinuous, and three-fifths the length of second abscissa of cubitus which in turn is two-thirds the length of first abscissa of cubitus.

Abdomen fulgid; elongate fusiform; with a thin and sparse vestiture of decumbent puberulent hair and with microscopically fine transverse aciculation. Second to penult tergites with distinct basal acarid chambers; ultimate tergite with a subopaque, very finely and closely punctate pygidial area of which the basal two-thirds is subequilaterally trigonal in shape, submarginate laterally, and concave discally, and the apical third drawn out into an elongate linear portion, sharply margined laterally, canaliculate discally, and rounded apically. Sternites with a transverse submarginal row of erect setulae.

Male. Unknown.

Remarks.—The closest relative of the present Californian species is the European form *curvitarsus.* I have seen no material of the latter, but the North American specimens of *foveolineatus* examined agree very closely with Kohl's excellent description and figures of that species.[36] Since certain widespread European species like *Euplilis clavipes* (L.) have been discovered in western North America,[37] while other forms such as *Rhopalum pedicellatum* Packard, 1867, and *Blepharipus parkeri* Banks, 1921, hitherto supposedly discrete Nearctic species, are now known to be conspecific with the European *Euplilis coarctata* (Scopoli), 1763,[38] and *Crossocerus (Ble-*

[36] Kohl: Ann. K. K. Naturhist. Hofmus. Wien, XXIX, pp. 326–328, figs. 306–310, 312–314, 316 (1915).

[37] I have examined series of this Pemphilid from various localities in Washington, Oregon and northern California. They agree perfectly with European specimens determined by Kohl as [*Crabro*] *clavipes* L.

[38] I find tbat upon comparing material of the common widespread North American form *Rhopalum pedicellatum* Packard, 1867, with European specimens determined by Kohl as [*Crabro* (*Rhopalum*)] *tibiale* F. [1798=*Euplilis coarctata* Scopoli, 1763], no significant difference exists

pharipus) ambiguus (Dahlbom), 1842,[39] respectively, it would not be surprising if, in view of the fact that save in a few minor details Kohl's description and figures of *curvitarsus* apply so well to the Nearctic material of *foveolineatus* before me, the North American form were to eventually prove identical with, or but racially distinct from, the European species. The solution of this problem, however, must await the discovery of the male sex of *foveolineatus* and comparison of Nearctic with Palaearctic material.

Specimens examined.—In addition to the type from Shasta County, I have seen another female from California, taken at Carrville in Trinity County on June 10, at an altitude of between 2400 and 2500 feet. This specimen agrees with the type in all essential particulars.

Distribution.—Although at present the only records of the present species are from the Mt. Shasta region in northern California, *foveolineatus* probably occurs over a much larger area in western North America. The distribution of the European *Tracheliodes curvitarus*, the closest kin of the Nearctic *foveolineatus*, is determined largely, according to Kohl,[40] by that of the ant, *Liometopum microcephalum*, upon which the wasps prey. Consequently, inasmuch as *foveolineatus* is known to occur within the range of *Liometopum occidentale*,[41] the North American counterpart of the Palaearctic *L. microcephalum*, it is not illogical to presume that *foveolineatus* attacks *L. occidentale*, and hence to infer further that its range is mainly conditioned by, and in all likelihood more or less coincident with, the distribution of this ant. If this assumption is correct, then *foveolineatus* is, like the ant *occidentale*, mainly a stenothermal psychrophile of the west coast Transition Zone.[42] Its range probably extends from central-western Oregon southward through the Cascade and Coast Ranges to the Transverse Ranges district[43] of southern California, and also along the western flanks of the Sierra Nevada Mountains.

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between the Nearctic and Palaearctic specimens and believe therefore that Packard's name should be recorded as a synonym of Scopoli's much earlier one.

[39] *Cf.* Pate: Notulae Naturae, no. 91, p. 8, footnote 4 (Sept. 11, 1941).

[40] Kohl: Ann. K. K. Naturhist. Hofmus. Wien, XXIX, p. 328 (1915).

[41] The North American *Liometopum occidentale* resembles the European L. *microcephalum* so closely that Emery originally described it as merely a variety of the Palaearctic species.

[42] According to Wheeler (1917, Proc. Amer. Acad. Arts & Sci., LII, p. 522) ". . . *L[iometopum] occidentale* is very abundant among live-oaks at low altitudes in the Coast Range of California but less common in the Sierras. It seems not to occur on their eastern slopes, judging from my inability to find it in the Lake Tahoe Region. Only a few colonies were seen in the Yosemite; at Wawona it was more abundant . . ." For detailed record of this ant, see page 521 (*loc. cit.*).

[43] The San Gabriel and San Bernardino Mountains.